The life-history of short-tailed shearwaters (*Puffinus tenuirostris*) in response to spatio-temporal environmental variation

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Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.

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Abstract

Ecological changes in the phenology and distribution of plants and animals mediated by changes in the environment are occurring across the globe and have been documented for a wide range of species. However, determining the specific mechanisms that affect the life-history parameters of organisms is typically difficult. Measuring population trends over time, and in relation to broad-scale environmental state, is one of the simplest ways of linking the effects of physical environmental variation to its direct effects on biological systems.

This study is concerned with describing key life-history parameters and population demography of a wide-ranging and abundant pelagic seabird, the short-tailed shearwater (*Puffinus tenuirostris*). The population demography of this upper-trophic consumer is investigated directly within the context of its spatio-temporal use of the marine environment and its response to environmental variation.

In this thesis I present data and analyses for:

1. *Population trends of short-tailed shearwaters and the sympatrically breeding little penguin (Eudyptula minor)* – Trends from a colony of short-tailed shearwaters at the southern most extent of their distribution were documented from 2003–10 and found to be declining at a rate of 15% per annum. A series of hypotheses were constructed to provide possible explanations for the observed trends including source-sink population dynamics, recreational 'mutton-birding', by-catch from fisheries, investigator effects, changes in onshore habitat characteristics, and distal changes in food source availability. In contrast little penguins were found to be increasing at a rate of 17% per annum with their increase attributed to the removal of feral cats from Wedge Island in 2003.
2. *The effects of investigator disturbance on short-tailed shearwaters and little penguins* – Researcher activities were monitored during the course of the study to identify any possible effects on rate of egg laying, chick survival or chick handling. No effect of the investigator was observed in short-tailed shearwaters for any of life-history attributes measured with the effect of investigators on little penguins unable to be conclusively determined.

3. *The spatio-temporal use of the Southern Ocean during the breeding season of short-tailed shearwaters* – Geo-location devices were deployed on 20 birds in the breeding seasons of 2004–05 and 2007–08. Foraging locations and behaviours were identified over a temporal scale encompassing the entire breeding season from the pre-egg laying 'honeymoon' period, to chick rearing. This study determined that trip characteristics changed significantly over the duration of the breeding season. Bimodal foraging strategies occurred once chicks had hatched and the duration of long trips contracted from 20.1 ± 10.6 days to 14.6 ± 2.2 days. Foraging occurred in a range of water masses from the Australian continental shelf to the Polar Frontal Zone with use of Southern latitudes increasing over the course of the breeding season.
4. *Identifying Annual variability in the diet of short-tailed shearwaters using stable isotope analysis* – Whole blood samples were collected over 4 breeding seasons and used to identify trophic foraging level and latitudinal foraging location. Inter-annual differences in diet were observed during the four breeding seasons with $\delta^{13}C$ and $\delta^{15}N$ values in 2004–05 and 2005–06 significantly higher than in 2006–07 and 2007–08. Despite the contrast in diet between seasons, there was no direct relationship detected between prey type and reproductive performance indicating that short-tailed shearwaters are flexible in their response to changes in prey availability.
5. *Influences of environmental variation on the population trend of short-tailed shearwaters*– After identifying specific spatio-temporal regions of importance, this information was used to link physical oceanographic parameters such as sea surface temperature (SST), primary productivity (Chla), wind speed and direction, sea surface height (SSH), sea surface height anomaly (SSHa) and ice edge extent to the decline in breeding short-tailed shearwaters. While no relationships were determined between chick survival and environmental variables, we detected a relationship between a decline in egg laying and an increase in pre-egg laying sea surface height anomaly (SSHa) in the Southern Ocean.

General discussion and recommendations for future research–Understanding the causal mechanisms driving changes in population demography is complex.

Changes are often subtle and may be interconnected. By utilising multi-dimensional approaches including telemetry, diet and physical oceanography, improvements can be made in determining the links between the marine environment and upper trophic consumers. As environmental changes may affect different demographic parameters and the response variables may be direct (*i.e.* an increase in adult mortality or a decrease in adults choosing to breed) or lagged (*i.e.* reductions in breeding success), it is likely that multiple processes are contributing to the decline of shearwaters on Wedge Island. This colony should continue to be monitored, in addition to others within the species distribution as only long-term data sets will determine if this is part of an oscillation in breeding numbers or a response to more long-lasting shifts in environmental conditions. Chick diets should be obtained in addition to adult diet corresponding to the pre-egg laying period. Marking of birds within the colony will assist in making stronger conclusions as to the effect of emigration. Further telemetry studies will aid in detecting inter-annual differences in foraging behaviours.

Thesis outline

With the exception of the introduction (current chapter) and the general discussion (Chapter 7), all chapters are self-contained and have been written as scientific papers. As a consequence there will necessarily be some repetition between chapters in the introduction and methodologies. I am the senior author on each paper in the thesis and have been responsible for the organisation and execution of field work, laboratory analysis and data analysis in the field seasons of 2004–05 to 2007–08 (four consecutive seasons). Data from the pilot study (2002–03) has been included in this work and two years of breeding data (2008–09, 2009–10) have been collected by an honours student and volunteers. As Chapters 2–6 contain multiple authors, I have used 'we' to refer to decisions or conclusions reached in the work, however in Chapters 1 and 7, I have used 'I'.

Declaration of contribution

Professor Mark Hindell (supervisor), Dr Clive McMahon (supervisor) and Dr Corey Bradshaw were involved in the initial experimental design and both Professor Hindell and Dr McMahon have made contributions to the papers in terms of discussion of content and critically reviewing drafts of the papers. Virginia Andrews-Goff (PhD candidate) was initially involved in the pilot study of the island and her data contribution has been acknowledged as Co-authorship in chapter 3. Owen Daniel (BSc Hons) was involved in deploying geo-location devices on short-tailed shearwaters in 2008–2009 and collecting blood samples in the same year. His contribution has been acknowledged as Co-authorship in chapters 4 and 5. Dr Ben Raymond was instrumental in obtaining the environmental data used in chapter 6 and is Co-author of this chapter.

Acknowledgements

Writing a PhD thesis is a bit like jumping out of a plane. It's so exciting on the way up, that you don't realise quite what a big decision you've made until you're in the air realising that it's an awfully long way to the ground and you've come just that little bit too far to change your mind. All you can do is hope that your parachute opens on the way down. That being said, the rush when you get to the ground safely makes it worthwhile in the end. It took quite a few parachutes to get me safely to the ground and therefore I apologise to the reviewers for what must be a necessarily long list of acknowledgements.

My long suffering supervisors Prof Mark Hindell and Dr Clive McMahon, whom I have given reason to bury their heads in their hands so many times and yet have remained a constant source of inspiration with their intelligence, patience, tolerance, humour and insight. If, at any point in the future, I end up as half the scientists that they are, I will consider myself successful.

The members of the formerly known A.W.R.U lab, particularly Mary-Anne Lea who has provided constant encouragement and new perspective on concepts that continued to elude me; Tim Reid for his statistical help and discussions of the nature of seabird population demography; Virginia Andrews-Goff for piloting the study; Ben Arthur for his assistance with the tracking work; and Mike Sumner for his amazing brain and ability to answer all my R questions.

All of the extraordinary volunteers who assisted with fieldwork during research years. Particularly, Cara Morris who walked over every centimetre of that island with me in order to set up the transects AND survived the horror trip of 50 kn winds, hail, torn tents and no gas stove. It's why we love field work. Also particular thanks to those that came back more than once: Dr Kathryn Wheatley, Louisa D'Arville, Tammy McGowan, Owen Daniel and my Dad.

The Holsworth Wildlife Fund who provided funding for the stable isotope analysis, and the Pacific Seabird Group and Lotek Wireless who provided the geo-location devices.

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Taryn Turner who knows how to use a semi-colon (the highest editorial accolade I can give) and was instrumental in editing during the last few weeks.

My colleagues and friends of the Port Arthur Historic Site Management Authority (PAHSMA) who allowed me to work on this thesis while I was supposed to be answering questions about Australia's most infamous convict prison (subsequently, I think some poor confused visitors may have left with the impression that seabird responses to environmental variability were a major part of 19th century convict life)

Marcus Salton who always managed to find the unfindable references; Lydia Hantke, my poor housemate who had to put up with me (but who could always be counted on for hysterical laughter and cups of tea). Also, thanks to Jo and Eric Jumper who lent me the laptop that this was written on in the aforementioned historic site. Thanks guys.

Here's one of those illuminating insights that you think should be really obvious but really isn't: No one can predict how they will respond to stressful situations. As one of those irritatingly cheerful and 'unflappable' creatures, I was horrified by the betrayal of my own body midway through candidature. The physiological symptoms of stress had me undergoing months of testing for everything from an

inner ear infection, to mitral valve prolapse and brain tumours. Without doubt I would have thrown the towel in completely were it not for a few understanding, generous and strong people who, when the cause was finally identified, refused to let me drop the bundle entirely. Judy McCarthy who would unceremoniously throw me into the car for a walk on the beach; Ilka Zimmer who was the first person to tell me it was okay to not have it together all the time; Julia Back for her constant encouragement and ability to make me laugh and Mel Andrewartha, my absolute rock and anchor without whom the last push would not have happened. There will never be enough words to express my gratitude.

Finally, this thesis is dedicated to my parents. My mother Jo and my father, Peter, who know me well enough to say 'it's okay if you don't finish' which made me determined that I would. My dad's enthusiasm for this project saw him traipsing all over Wedge Island with me and eventually taking on responsibility for the continuation of the data collection. Their support, painstaking editing and constant belief in me are incredibly humbling.
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Chapter 1

General Introduction

Ecological changes in the phenology and distribution of plants and animals mediated by changes in the environment are occurring across the globe and have been documented for a wide range of species (Parmesan 2006). However, determining the specific mechanisms that affect the life-history parameters of organisms is typically difficult. Environmental changes may affect different demographic parameters (Weimerskirch et al. 2003) and the response variables may be direct (i.e. an increase in adult mortality or a decrease in adults choosing to breed) or lagged (i.e. reductions in breeding success) (Wooller et al. 1992). Marine environments are typically dynamic and resources may be patchily distributed (Mann & Lazier 2006). This study is concerned with describing the life-history parameters and population demography of a wide-ranging and abundant pelagic seabird, the short-tailed shearwater (*Puffinus tenuirostris*). The population demography of this upper-trophic consumer is investigated directly within the context of its spatio-temporal use of the marine environment and its response to environmental variation.

Life-history, environmental parameters and marine predators

The basic hypothesis underlying the analyses of life-history traits is that variation is constrained in large measure by a trade-off between traits (Stearns 1992). Life history traits are constrained by genotype, phenotype and environmental influences that may be bio-chemical, bio-physical or bio-mechanical. Demographically, reproductive effort can be divided into two relationships: that between reproductive effort and survival and that between reproductive effort and number of offspring (Roff 1992). For many upper trophic consumers in highly stochastic environments, environmental pressures favour the evolution of species in which the trade-off between reproductive effort and survival is implemented. Known as K selected species, they typically display high adult survival, low fecundity, delayed onset of reproduction, and high levels of parental care of their offspring (Pianka 1970).

Many pelagic seabird species are regarded as K selected. They have long life-spans (15–70 years) and are often wide-ranging. Therefore factors that affect their

life-history and population demography integrate both wide temporal and spatial scales and are generally within highly variable environments (Smith et al. 1999). Subsequently, the parameters that drive changes in population structure and size are not always easy to disentangle because of the complex relationships between key life-history traits such as survival, fertility and environmental changes. (Jenouvrier et al. 2003).

The nature of relationships between physical and biological processes is subtle and complex. This is because not only do physical processes define structures within which biological processes occur, but they also influence the rate of biological processes indirectly via energy flow (Mann & Lazier 2006). Subsequently, when attempting to understand the processes that ultimately affect the performance of upper trophic consumers, knowledge is needed of the physical environment in which they reside. Measuring the physical properties of marine environments has improved in the last few decades with the development of remote sensing technologies that accurately measure a suite of oceanographic parameters. Measuring the physical environment provides the means by which to describe natural global climate patterns conditions such as El Nino-Southern Oscillation (ENSO) events (Jaksic 1998), the Antarctic Circumpolar Wave (ACW) (White & Peterson 1996) and the Pacific Decadal Oscillation (PDO) (Zhang et al. 1997). This also establishes base line data against with which to assess both natural variability and anthropogenic change. However, high latitude data has typically been of poor quality with low spatial and temporal resolution (Sumner et al. 2003) and direct sampling within these latitudes remains difficult due to the size and inhospitable nature of the environment. Nonetheless, information on physical oceanographic processes is a crucial component of any biological study.

Variation in climatic conditions affects the location and abundance of primary productivity (i.e. phytoplankton) which flows on to the distribution and abundance of secondary consumers (grazers) and ultimately to the vertebrate predators (Hindell et al. 2003). However, even for commercially exploited species, survey based data of marine invertebrates and fish, that can link the physical environment to the response of upper trophic consumers, are typically scarce in higher latitudes. In addition, these data may be biased due to behavioural characteristics

such as ship avoidance which has been demonstrated in some pelagic fish (Hunt Jr et al. 1990; Durant et al. 2009). Recent developments in monitoring technology are allowing the measurement of some oceanographic physical parameters in situ and these data are proving to be rigorous and are augmenting the data obtained by conventional means (McMahon et al. 2005).

Variation within the physical environment is not the direct mechanism by which upper trophic consumers may be affected. Rather, environmental variation is likely to exhibit the most influence through indirect factors acting on the nature and extent of breeding habitat, on foraging habitat or on the distribution and abundance of food supplies (Newton 1998). The interactions between environmental parameters and predators are likely to have shaped species specific breeding and survival strategies (Jenouvrier et al. 2003). Therefore, it is the tight trophic interaction between consumers and resources that provides the best opportunity to understand the mechanisms driving the response of upper level predators (Durant et al. 2009). Identifying causal links between seabird population demography and environmental variation is typically difficult and a recent review by Durant et al. (2009) has highlighted some of the considerations when attempting to link the response of seabirds with their biotic and abiotic environments:

Correlation between environmental variability and population demography does not necessarily imply causation. For example, due to plasticity in foraging behaviour, prey abundance may be over-estimated when breeding success is high and underestimated when breeding success is low;
Most measures currently employed only refer to the bottom-up effect of environmental variability and largely ignore top-down forcing of the regulation of populations via competition and predation (Ainley et al. 2007; Nicol et al. 2007);
Seabirds are generally long-lived and exhibit delayed onset of reproduction and therefore effects of environmental variability may demonstrate lagged effects (Thompson & Ollason 2001);
Individuals may demonstrate plasticity in their response to environmental change and compensate for localised perturbations by switching diet or foraging range which may mask the detection of responses (Durant et al. 2004);

Sampling error may be inherent throughout the duration of long-term studies and methodology is not consistent (Thomas 1996; Holmes & Fagan 2002); and
Few studies take into account the possible effect of researchers on their measured parameters.

Measuring population trends

The complexity of pelagic ecosystems ensures that factors influencing population demography are driven by multiple mechanisms and subsequently multi-dimensional studies are required to identify linkages (Micol & Jouventin 2001). However, measuring population trends over time, and in relation to broad-scale environmental state, is one of the simplest ways of linking the effects of environmental variation to their direct effects. The most efficient procedure involves repeated annual censuses of the same site against which changes in abundance can then measured (Thomas 1996). However, detecting changes in population trends may not be straightforward, and long-time series are often needed in order to assess the true directionality of trends (deLittle et al. 2007).

The efficacy of detecting changes, particularly declines, is increased by monitoring a species at the periphery of its range. Wilcove and Terborgh (1984) proposed that declines can manifest as 1) range contraction only, 2) range contraction and reduced densities in marginal and optimal habitat, 3) reduced densities in marginal habitat with no range contraction and 4) reduced densities in marginal and optimal habitat with no range contraction. Therefore declines may be detected at the periphery first even if no reductions in range or density are detected from the centre of the distribution. More recent studies have also suggested that improvements can be made in the ecological interpretation of the interactions between seabirds and their environments with the inclusion of telemetry studies. These facilitate the detection of foraging patterns (such as area-restricted search) that can help to identify important foraging areas (Tremblay et al. 2009).

Changes in the physical environment of the Southern Ocean have intensified in the last 20 years (Sokolov & Rintoul 2009a). As these changes are already affecting lower trophic consumers (Atkinson et al. 2004), it follows that upper trophic

consumers may also be exhibiting changes in response to increasing environmental variation. Of most concern is the possible effect of environmental variation on species that are already threatened. However, given that studying endangered or threatened species can be difficult, the use of more common species, e.g. short-tailed shearwaters, occupying similar spatial and trophic scales can be an effective proxy (Sykes et al. 1990).

The study species

Short-tailed shearwaters are a medium size (500–600 g) burrow-nesting Procellariiformes seabird. They breed in colonies ranging in size from a few hundred to millions of birds throughout the extent of south-east Australia with the centre of the breeding distribution in Bass Strait at around 40° S, 160° E. The most recent estimate of their total population size is 23 million birds with an estimated 18 million birds breeding around the coast of Tasmania (Skira 1991). Due to their large biomass they act as significant consumers of marine resources and forage on a wide range of species including coastal, sub-Antarctic and Antarctic crustaceans such as Nyctiphanes australis, Euphausia vallentini, Euphausia superba as well as squid and myctophid fish (Skira 1986; Cherel et al. 2005).

Short-tailed shearwaters are trans-equatorial migrants and are highly synchronous breeders. Breeding adults generally arrive in the breeding colonies during the last week of September, re-establish pair bonds and scratch out burrows. Mating occurs during this time, after which the adult birds leave the breeding colonies and undertake a 'honeymoon' foraging trip to re-establish body condition prior to incubation and chick rearing (Serventy 1967). Egg laying occurs in the last week of November (mean November 27) at which point the male bird undertakes the first 10–14 day incubation shift. Eggs are incubated for a mean of 53 days and hatch around the 3rd week of January. Once eggs hatch and chick rearing commences, shearwaters employ a bimodal feeding strategy, alternating between a series of short trips close to the breeding colony to provision chicks and long trips that exploit distant resources for the self-provisioning of the parents (Weimerskirch et al. 1994). The chicks are fed until late March or early April during which time they

may achieve masses of over 1 kg, effectively twice the average adult body weight (Serventy 1967; Hamer et al. 1997). Adults then depart the breeding colony and commence a migration through the Pacific Ocean to the Bering Sea. The closely related sooty shearwater (*Puffinus griseus*) that undertakes the same migration has been reported to travel distances of > 30 000 km during this migration (Shaffer et al. 2006). The chicks then fast in the burrows until adult plumage develops and then proceed to undertake the same migration as the adults, departing in late April, early May. Birds exploit the Arctic marine resources and demonstrate foraging site fidelity during the austral winter (Baduini et al. 2006) before returning to the breeding colonies the following September.

Due to their high biomass, short-tailed shearwaters are listed as 'Least Concern' by the International Union for Conservation of Nature (IUCN). However, over the last few decades, 62 out of 131 Procellariiformes (albatrosses and petrels) species have demonstrated widespread declines, and are now considered as threatened, vulnerable, or endangered according to the IUCN red list (Baillie et al. 2004). The nature of the declines in the Procellariiformes is complex and has been attributed to a wide range of factors including habitat loss, predation by feral animals, changes and decrease in prey availability, by-catch from fisheries and climate change (Weimerskirch & Jouventin 1987; Boersma 1998; Micol & Jouventin 2001; Granadeiro et al. 2006; Priddel et al. 2006; Stevenson & Woehler 2007; Delord et al. 2008; Scott et al. 2008).

The study site

The selected study site needed to occupy a location on the periphery of the breeding range of short-tailed shearwaters and be known to have a moderate population of breeding birds. Wedge Island (43° 07' S, 147° 40' E) is a small island situated 1 km from Tasman's Peninsula in the south-east of Tasmania. The island is approximately 43 hectares in size, 1.3 km long, 0.55 km wide at its widest point and oriented north to south (Brothers et al. 2001).

Geologically, it is comprised of Jurassic dolerite and the vegetation is a mixture of native species including succulents such as native spinach (*Tetragonia*

implexicoma) and pigface (*Carpobrotus rossii*), grasses such as *Poa poiformis* and *Lomandra longifolia* and shrubs such as the kangaroo apple (*Solanum laciniatum*) and saltbush (*Rhagodia candolleana*). Some remnants of introduced vegetation such as geraniums, stinging nettle and blackberries are also present (Smith 2003). The island was used for sheep grazing from the early 1900's until their removal in 1986 and while rabbits were prevalent during the sheep grazing period, the introduction of a feral cat population removed them from the island entirely. The cat population persisted at low numbers until their removal from the island in 2003.

Aside from short-tailed shearwaters (*Puffinus tenuirostris*), other known species on the island include the little penguin (*Eudyptula minor*), the swamp harrier (*Circus approximansi*), the white-bellied sea eagle (*Haliaeetus leucogaster*), and three species of reptile; the spotted skink (*Niveoscincus ocellatus*), metallic skink (*Niveoscincus metallicus*) and mountain dragon (*Rankinia diemensis*). The study site is towards the most southerly extent of the distribution of short-tailed shearwaters in Tasmania (Skira et al. 1996) and given the size of the island, it is one of the few colonies that can be measured in its entirety. A pilot study of population size conducted in 2003, determined the breeding population of short-tailed shearwaters as 36 569 ± 7291 breeding pairs.

Aims and thesis structure

The overall aim of this study was to measure the life-history attributes of short-tailed shearwaters at the southern most extent of their breeding distribution, and to relate this to variability of marine resources. To achieve this, I studied the population of short-tailed shearwaters on Wedge Island (43° 07' S, 147° 40' E) between the austral summers of 2003–09. There were five specific objectives of the study, each the subject of a chapter of the thesis.

Chapter 2 aims to measure and describe the population trends of the short-tailed shearwater (*Puffinus tenuirostris*) and the sympatrically breeding little penguin (*Eudyptula minor*). The trends will then be related to intrinsic effects such as density dependence. Onshore habitat characteristics including the stability of the substrate, vegetation cover and possible poaching effects from recreational 'mutton-birding' will be explored. A series of hypotheses to describe the trends will then be formulated for further exploration.

Chapter 3 specifically investigates the effect of investigators on the key life history parameters; egg laying, chick survival and chick growth.

Chapter 4 describes the spatio-temporal use of the Southern Ocean by breeding short-tailed shearwaters using archival geo-location (GLS) tags. Specifically this chapter aims to detect behavioural foraging modes such as area-restricted search and to describe the most important foraging areas for short-tailed shearwaters during the breeding season.

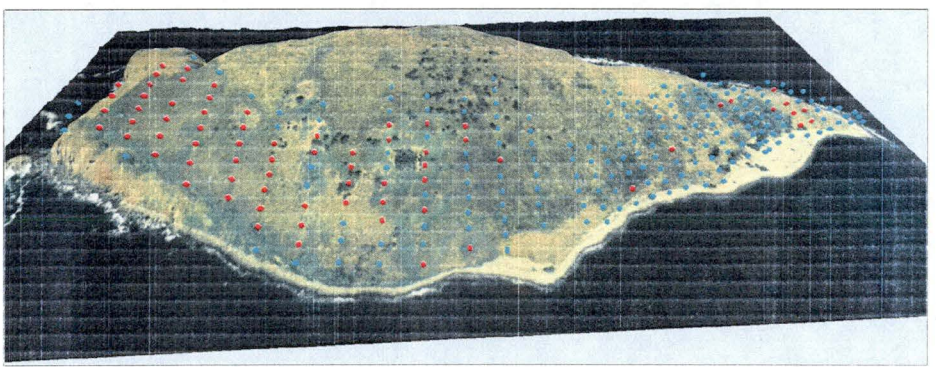
Chapter 5 uses stable isotope analysis as an inference of diet with the aim of detecting both inter- and intra- annual differences in prey consumption. Additionally this chapter is used to support the findings from the GLS study by comparing latitudinal estimates of foraging location derived from $\delta^{13}C$ values with the locations obtained from GLS.

Chapter 6 is a continuation of the previous chapters and aims to explore one of the hypotheses suggested in Chapter 2; that observed population trends are

correlated with environmental variation. Using geographical foraging ranges identified in Chapter 4, a number of physical oceanographic parameters are analysed for corresponding trends in both breeding effort and breeding success. This chapter discusses possible biological mechanisms by which observed changes in the physical oceanographic environment can affect upper trophic consumers.

Chapter 7 is the synthesis of the thesis and places the research within the context of research in other species and explores the possible contributors to the observed trends in terms of density dependent effects and environmental influences. The limitations of the study are discussed in context and I then make future recommendations for continued research in this population.

Chapter 2



Chapter 2

Contrasting population trends in two sympatric seabirds (short-tailed shearwaters, *Puffinus tenuirostris* and little penguins, *Eudyptula minor*) in south-east Tasmania

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Abstract

Describing population trends is a simple way of linking environmental factors to their direct effects, particularly in relation to animals that occupy high trophic niches such as seabirds. Between the austral summers of 2003 and 2010 the number of breeding short-tailed shearwaters *Puffinus tenuirostris* on Wedge Island in Tasmania, Australia declined from 36 569 ± 7291 to 12 602 ± 1697 breeding pairs representing a mean exponential decline of 15% per annum. Conversely, little penguins, *Eudyptula minor* also breeding on Wedge Island, increased from 480 ± 415 to 1020 ± 228 representing an exponential increase of 17% per annum. The most likely explanation for the increase in the breeding population of little penguins is the removal of the feral cat population from the island in 2003. The decline in breeding shearwaters is much more difficult to explain, although a breakdown of two individual shearwater colonies on the island revealed that only the largest colony with the highest density of burrows was declining. While determining a definitive reason for this population reduction is outside the scope of this paper, we discuss a number of possible hypotheses including source-sink population dynamics, recreational 'mutton-birding', by-catch from fisheries,

investigator effects, changes in onshore habitat characteristics, and distal changes in food source availability.

Introduction

Quantifying population trends of animal species is essential to understanding dynamic ecosystems and the potential influence of anthropogenic factors on those systems. Measuring population trends can provide invaluable information as to whether or not a population may be in decline and therefore what steps need to be taken in order to construct a rigorous and carefully thought out hypothesis for describing the observed trends (Caughley & Gunn 1996) while recognising that the mechanisms underlying population trends can be confounded and difficult to isolate (McMahon et al. 2009).

In the last few decades, 62 out of 131 Procellariiforme (albatrosses and petrels) species have demonstrated widespread declines, and are now considered as threatened, vulnerable, or endangered according to the IUCN red list (Baillie et al. 2004). These are species that range widely across the world's oceans and integrate environmental changes over wide ranges. The Sphenisciformes (penguin) is an endemic Southern Hemisphere taxa that is diverse (17 species) and ecologically important (Croxall & Lishman 1987). The penguins have also been adversely affected by recent changes in their environment so that 10 out of the 17 taxa are currently listed as endangered or threatened (Baillie et al. 2004).

The nature of the declines in both groups of seabirds is complex and has been attributed to a wide range of factors including; habitat loss, predation by feral animals, changes and decrease in prey availability, by-catch from fisheries and climate change (Weimerskirch & Jouventin 1987; Boersma 1998; Micol & Jouventin 2001; Granadeiro et al. 2006; Priddel et al. 2006; Stevenson & Woehler 2007; Delord et al. 2008; Scott et al. 2008). Given that studying endangered or threatened species can be difficult, the use of more common species occupying similar spatial and trophic scales can be an effective proxy (Sykes et al. 1990). Two species that do not feature on the IUCN red list are the short-tailed shearwater *Puffinus tenuirostris* and the little penguin *Eudyptula minor*. As such,

they are ideal species to study in an attempt to determine the mechanisms driving population change without the likelihood of negative effects on the populations.

Short-tailed shearwaters are trans-equatorial migrants that breed in large colonies in the southern parts of Australia from September to March and then migrate to the Bering Sea during the austral winter. Due to their high biomass they act as upper trophic consumers in the Southern Ocean during the breeding season and feed mostly on crustaceans such as *Nyctiphanes australis*, *Euphausia superba*, squid and myctophid fish which they travel frequently to Antarctica to obtain (Weimerskirch & Cherel 1998). They are considered to be one of the most prolific birds in the southern hemisphere with an estimated global population of 23 million birds (Skira 1991). Little penguins, often breed sympatrically with short-tailed shearwaters and are also upper trophic predators of the coastlines of southern Australia and New Zealand. They feed predominantly on mid-water schooling prey, such as anchovy sp. and pilchard sp. (Stahel et al. 1987). Although, in the south-east of Australia, little penguin diet has changed due to a mass mortality of pilchards in 1996 and now incorporates such species as juvenile red cod (*Pseudophycus sp*), barracouta (*Thyrsites sp.*) and blue warehou (*Seriolella sp.*)(Chiaradia et al. 2003) Their global population is believed to be stable at around 350-360 thousand breeding pairs (Marchant et al. 1990)

Measuring the population trends of these species concurrently provides information from two habitats (i.e. offshore and inshore foraging areas) and may provide insight into some of the processes that are impacting on survival and driving the population trends. As little penguins during breeding are restricted in their foraging ranges to within approximately 40km of their nest site, they provide information on a local scale in terms of prey availability and abundance. In contrast short-tailed shearwaters with their trans-hemispheric distribution provide information at a much wider scale.
In this manuscript, we aim to i) quantify the population trends of these sympatric species from a population in southern Tasmania, ii) determine if vegetation is affecting the population trends, iii) determine the effect of recreational harvesting of short-tailed shearwaters on the population trends, iv) determine the effect of the

investigator on the rates of egg laying and v) asses further agents of decline to formulate hypotheses for future work.

Methods

Wedge Island (43° 07' S, 147° 40' E) is a small island located off Tasman's Peninsula in the south-east of Tasmania, Australia (Fig. 2.1). This island is near the southern limit of the breeding range of short-tailed shearwaters, at the southern limit of Australian populations of little penguins, and importantly is at the southern extremity of the East Australia Current (EAC) which potentially subjects these animals to a greater degree of environmental variation than occurs on the Bass Strait islands where the majority of previous work on these animals has been undertaken.

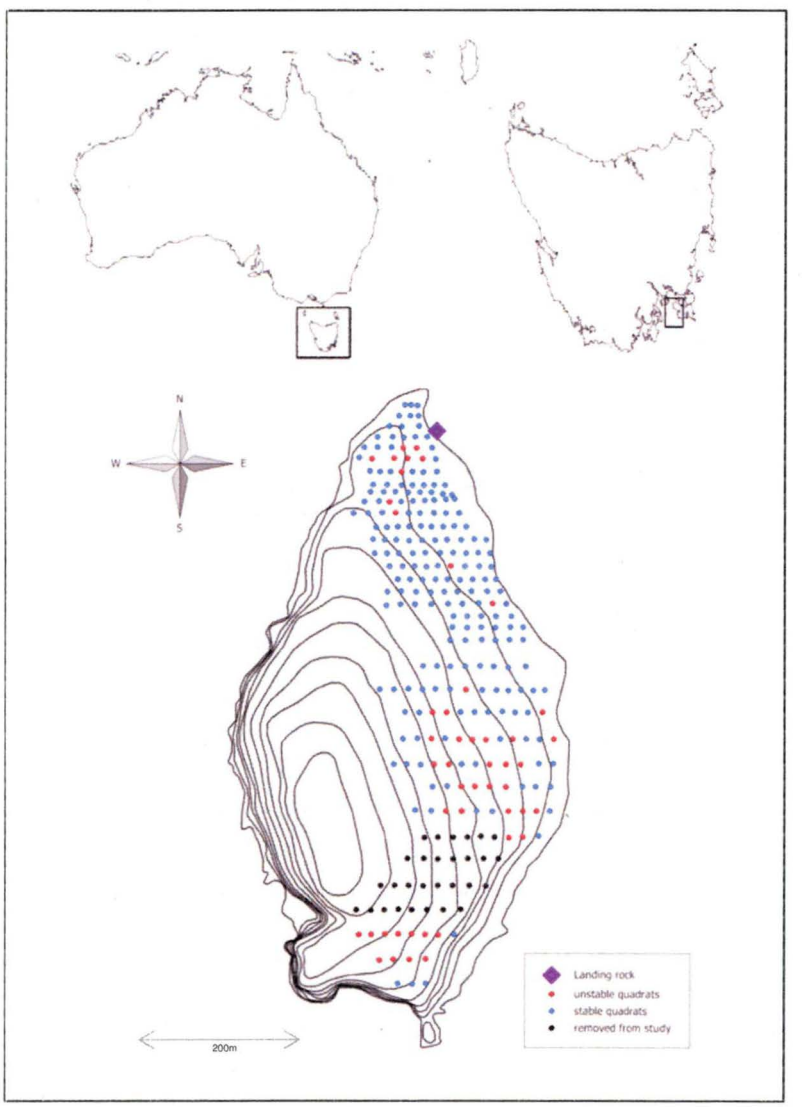

Fig. 2. 1. Location and distribution of quadrats on Wedge Island in relation to Tasmania and Australia..

Field work was undertaken during October–April 2002–03, 2004–05, 2005–06, 2006–07, 2007–08, 2008–09, 2009–10. The 2002–03 season was regarded as a pilot study with lower sampling effort than the subsequent seasons. Trips occurred monthly, starting on the 10th (± 5) of the month and the duration of the trips was 6 days (± 2). All seasons will subsequently be referred to by their finishing year, for example 2002–03 will be referred to as the 2003 season.

To determine population size, the island (1.6 km× 0.8 km – at its widest point) was divided into 35 east/west line transects (length 40-450m, Fig. 2.1). A stratified sampling regime to count birds was used: transects 1-20 being in the area of highest little penguin density, were 25m apart, and transects 21-35 placed 50m apart. Circular sampling units (quadrats) to reduce edge effects were placed at 20m intervals on transects 1-20 to increase sampling effort in the little penguin colony, and at 25m apart on transects 21-32 which contained only shearwaters. The end point of each transect was determined as the last quadrat past the last burrow. All burrows within a 2m radius of the sampling unit centre were individually marked using flag markers (plastic tabs mounted on wire staves) with the size of quadrat enabling detection of every burrow. A total of 241 quadrats containing 674 shearwater burrows were marked in this way during the 2004 season; of these 473 burrows (transects 17–35) were checked twice to monitor survival of chicks (once in December to establish laying success and once in April to establish fledging success). The remaining 201 burrows (transects 1–16) were checked monthly for a total of seven times per season. Transects 1–16 were chosen for the intensively checked area due to the smaller colony size and stable substrate of this areas perimeter which allowed for access without frequently traversing unstable area.

Burrow contents were observed without handling animals by using a custom made 'burrow scope' (a lipstick camera with infra-red lights attached to a 3m flexible tube and wired to a 87.5mm colour monitor). Each quadrat was categorised as stable or unstable based on the fragility of the burrows and the surrounding substrate. A quadrat was considered unstable if there was soil movement of the burrow roof in greater than 2 burrows, and otherwise stable. Vegetation was recorded as

percentage cover of each species in 2005 and 2009 and the location of the quadrats was recorded using a handheld GPS.

A handheld GPS was also used to map the colony perimeter of short-tailed shearwaters in 2004, 2007 and 2008. This information was entered into GIS software (Manifold) and the colony area calculated. Burrow density, quadrat position and occupation were mapped, and a surface was created using burrows per quadrat as the measure of height and Kriging interpolation at radius of 1arcsecond to map burrow density.

Due to the far lower density of little penguins, the colony area was calculated as a polygon using the transect lengths for the distribution of occupied penguin burrows.

Statistical Methods

Mean population density for both species was calculated as the sum of mean density of active nests per quadrat divided by the total number of quadrats.

$$\overline{D} = \frac{\sum_{q=1}^{n} D_q}{n}$$

The standard error of the mean density was calculated as:

$$SE\overline{D} = \frac{SD\overline{D}}{(\sqrt{n})}$$

Where $SD\overline{D}$ = standard deviation of mean population density and n = number of quadrats.

The total population of breeding pairs was estimated as the product of mean birds and the total area of the colony.

$$X = \overline{D} A_{WI}$$

Where X = total population, $\overline{D}$ = mean population density and A_{WI}= total area of colony on Wedge Island.

The natural log of the mean was calculated (Caughley & Gunn 1996) as it allows determination and comparison of rates of change between samples and the population was subsequently plotted against year with the regression line added.

There are two distinct shearwater colonies on Wedge Island. We compared the population numbers and trends for both colonies because small colonies have a greater perimeter to area ratio than larger colonies, and hence greater potential for edge effects to influence population growth rates (Aebischer & Coulson 1990). Moreover, the smaller colony was more accessible from the only landing point on the island than the larger colony and dividing the analyses between the two colonies was important to test the hypothesis that "mutton birding" (hunting nearly fledged chicks) may be responsible for any observed changes in population size and growth.

The rate of change in occupied burrows between 2005 and 2010 was plotted against burrow density in 2005 to quantify the relationship between the population trends and the density of burrows. This observed rate of change was compared to a predicted rate of decline calculated from the logarithmic regression of both colonies. As rate of change potentially contains high numbers of zeroes (no change observed) a 2 dimensional kernel density estimate plot was calculated in R to demonstrate concentration of points.

Vegetation types were identified using a Bray Curtis similarity matrix (4^{th} root transformation, complete linkage) with separation between groups at 10% difference. A chi-square test was used to ascertain if selection for vegetation type occurred, a generalised linear model (glm) (binomial distribution, logit link) used to identify selection for individual vegetation types with this information displayed as a vegetation map of the island using voronoi neighbours in Manifold.

Results

Quadrats were initially laid over the entire island, however, transects 32, 31, 30 and half of 29 were too unstable to traverse without potential damage to the substrate and burrows so these transects were excluded from the study and have never been used in calculating the population trends (Fig. 2.1).

The perimeter of the short-tailed shearwater colony (both sub colonies combined) was similar for each of the three years that it was monitored (Table 2.1), and the associated variance is most likely due to error in the GPS estimates (dependent on cloud cover, number of satellites passing, tree cover etc). Therefore, mean colony area for the three years was used to estimate the population sizes. However, the colony area for the little penguins however increased each year; this increase was compensated for and calculated by adding additional transects to the original colony perimeter polygon.

The number of shearwaters laying eggs each year has decreased significantly since 2003, with a significant logarithmic decline in the order of 15% per annum ($y = -15.3 \pm 0.01x + 317.5 \pm 22.5$, $F_{1,5} = 186.3$, $p = <0.01$, $R^2 = 0.969$) (Fig. 2.2a). This equates to a loss of approximately 6848 birds per annum. Penguins however, showed the reverse of this trend with a significant increase at the rate of 15% per annum ($y = 15.4 \pm 0.03x - 303.8 \pm 70.8$, $F_{1,4} = 24.38$, $p<0.01$, $R^2 = 0.8239$) (Fig. 2.2b).

When the colonies of shearwaters were analysed separately and the individual population trends compared, the two colonies showed markedly different patterns (Fig. 2.3). The smaller colony (mean of 3154 ± 877 pairs) remained stable over the study period ($F_{1,5} = 0.376$, $p = 0.57$, $R^2<0.001$) although the number of eggs laid varied between years. However, the larger colony decreased by 17.5% during the study ($y = -17.5 \pm 0.02x + 361.4 \pm 44.3$, $F_{1,4} = 62.96$, $p<0.01$, $R^2 = 0.912$) declining from 33 477 ± 6772 to 10 629 ± 1713 (Table 2.1). If the decline uniformly affected all breeding birds i.e. was density independent, we would expect to see a uniform decrease in occupied burrows throughout both colonies on the island. In

Table 2. 1. The estimated bird densities and colony areas of short-tailed shearwaters and little penguins on Wedge Island from 2003 to 2010 inclusive.

Year	quadrats	occupied quadrats	mean density m² colony 1 ± SE	mean density m² colony 2 ± SE	colony 1 m²	colony 2 m²	mean penguin density m²	penguin colony m²
2003	270	62	0.148 ± 0.235	0.250 ± 0 240	20963	133719	0.011 ± 0.027	55373
2005	241	98	0.108 ± 0.0187	0.216 ± 0.024	40987	131232	0.008 ± 0.002	50406
2006	241	92	0.051 ± 0.008	0.207 ± 0.021	N/A	N/A	0.013 ± 0.002	54436
2007	241	85	0.087 ± 0.015	0.173 ± 0 024	41762	130823	0 017 ± 0.003	54436
2008	241	74	0.076 ± 0 014	0.121 ± 0.022	Na	Na	0.016 ± 0.004	62000
2009	241	68	0.063 ± 0 018	0.097 ± 0.018	42889	130057	0.015 ± 0.003	72434
2010	241	65	0.067 ± 0.004	0.082 ± 0.013	N/A	N/A	N/A	N/A

Table 2. 2. Vegetation types and numbers of occupied quadrats of each type with descriptions referring to the dominant vegetation or habitat in each quadrat.

Vegetation	Description	Quadrats 2005	Quadrats 2006	Quadrats 2007	Quadrats 2008	Quadrats 2009	Quadrats 2010
1	Sand	23	18	20	21	12	15
2	*Lomandra longifolia*	16	17	13	12	14	12
3	*Solanum lacıniatum*	14	13	10	7	8	5
4	*Tetragonia implexicoma*	34	35	35	33	21	24
5	*Poa poaformis*	8	7	6	5	4	7
6	*Eucalyptus* sp	1	1	1	1	1	1
7	*Rhagodia candolleana*	2	1	1	1	1	0
8	*Allocasuarina* sp.	0	0	0	0	0	0
9	Cliffs or boulders	0	0	0	0	0	0

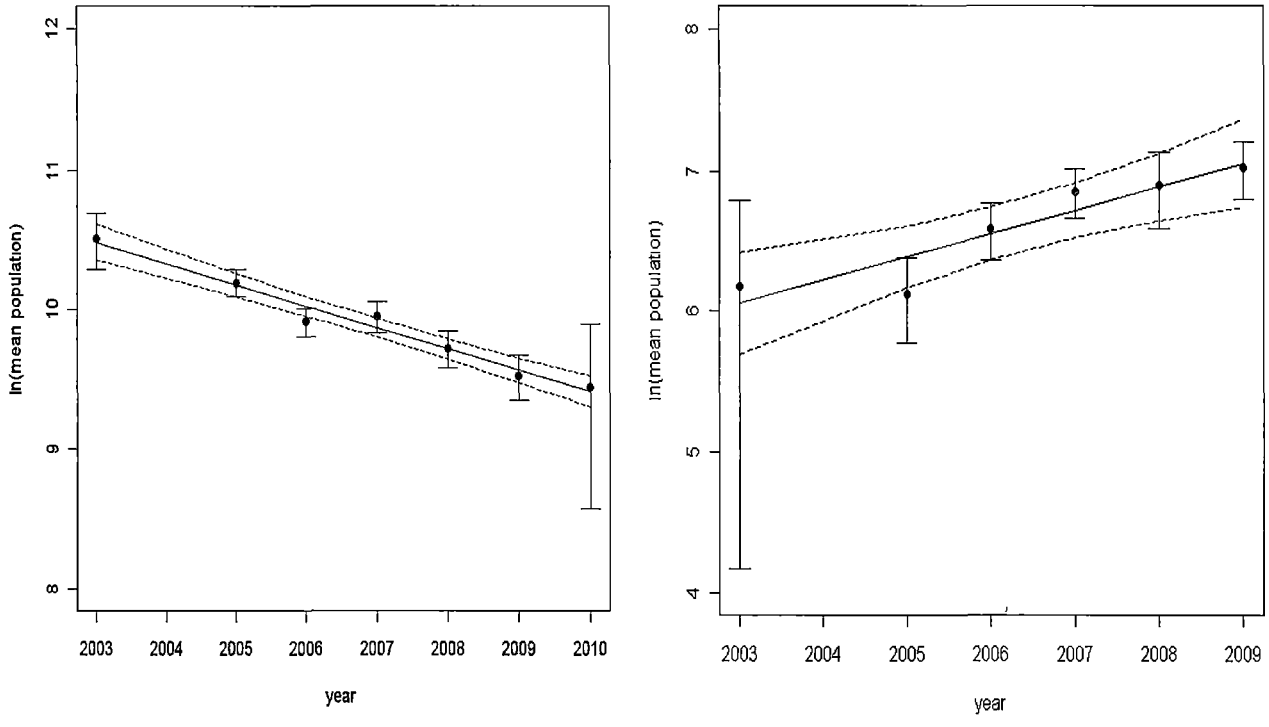

Fig. 2. 2. Population trend of a) short-tailed shearwaters and b) little penguins on Wedge Island for a 7 year data set (for sample sizes see table 2.1). Dotted lines represent the 95% confidence interval of the mean population trend (solid lines). Error bars are individual standard errors for each yearly estimate.

order to test density dependence, the rate of change of occupied burrows between 2005 and 2010 plotted against burrow density in 2005 was compared to the predicted decline in burrow density using the 15% figure calculated by linear regression (Fig. 2.4). This shows that the decline is not uniform, occurring more strongly in higher density areas of the colonies (Fig. 2.5). The 95% confidence intervals demonstrate that there is a high number of zeroes (implying no change in occupied burrow density between 2005 and 2009) and this is also demonstrated in the kernel density plot.

The Bray-Curtis similarity matrix identified nine different vegetation types at >90% difference, six of which are used by breeding birds (Table 2.2). Shearwaters predominantly used vegetation associations ($\chi^2 = 22.23$, df = 7, p = 0.003) comprising sand and Poa grasses (vegetation type 1), and *Tetragonia implexicoma* (iceplant) (vegetation type 4) (Fig. 2.6). With the decline in density, there was a subsequent reduction of occupied quadrats in vegetation types 1 and 4 (Table 2.2). However, when assessed during the last season of data collection, the vegetation types themselves did not alter significantly enough to change the vegetation groupings in any way.

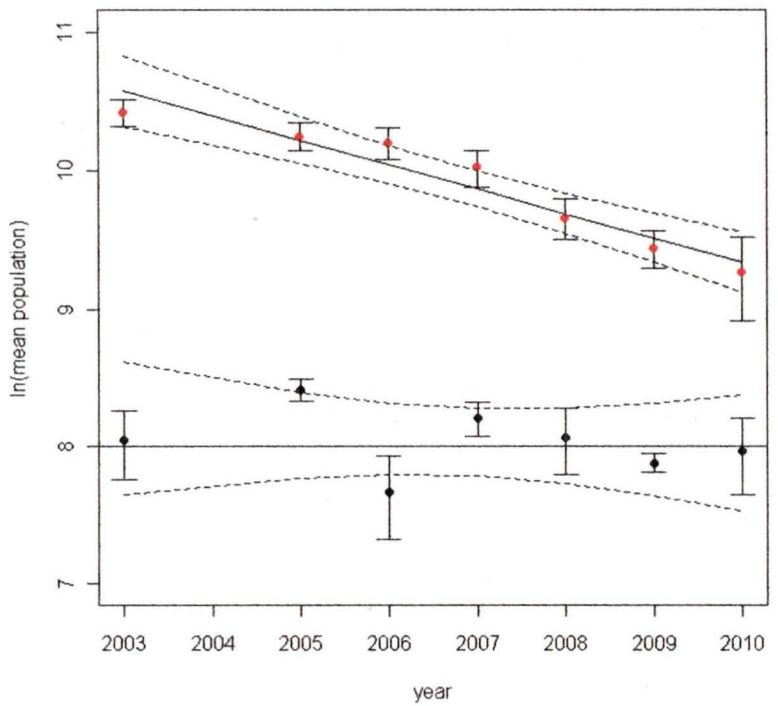

Fig. 2. 3. By colony breakdown of population trends for short-tailed shearwaters 2003-2009 (for sample sizes see table 2.1). Dotted lines represent the 95% confidence interval of the mean population (solid lines). Error bars are individual standard errors for each yearly estimate.

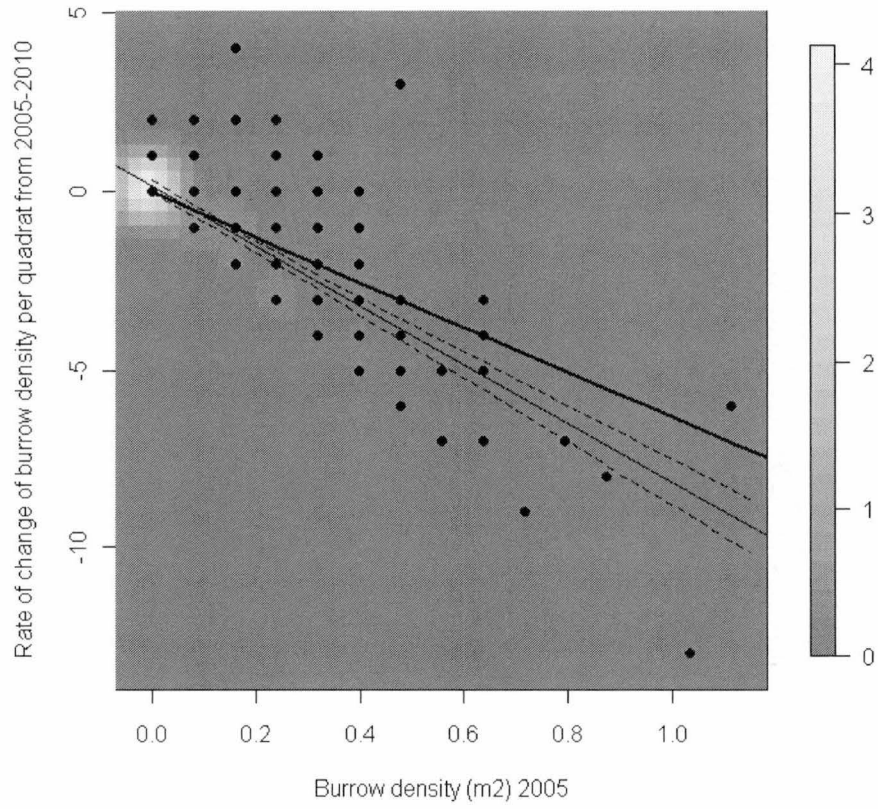

Fig. 2. 4. 2D kernel density plot describing the rate of change of occupied burrows from 2005 and 2009 against burrow density (m^2) of occupied burrows in 2005 when occupancy was highest. Regression line shows 95% confidence intervals and a greater rate of decline in the denser part of the colony. The weighted line is predicted exponential change of –15% if the decline was occurring uniformly throughout the colony.

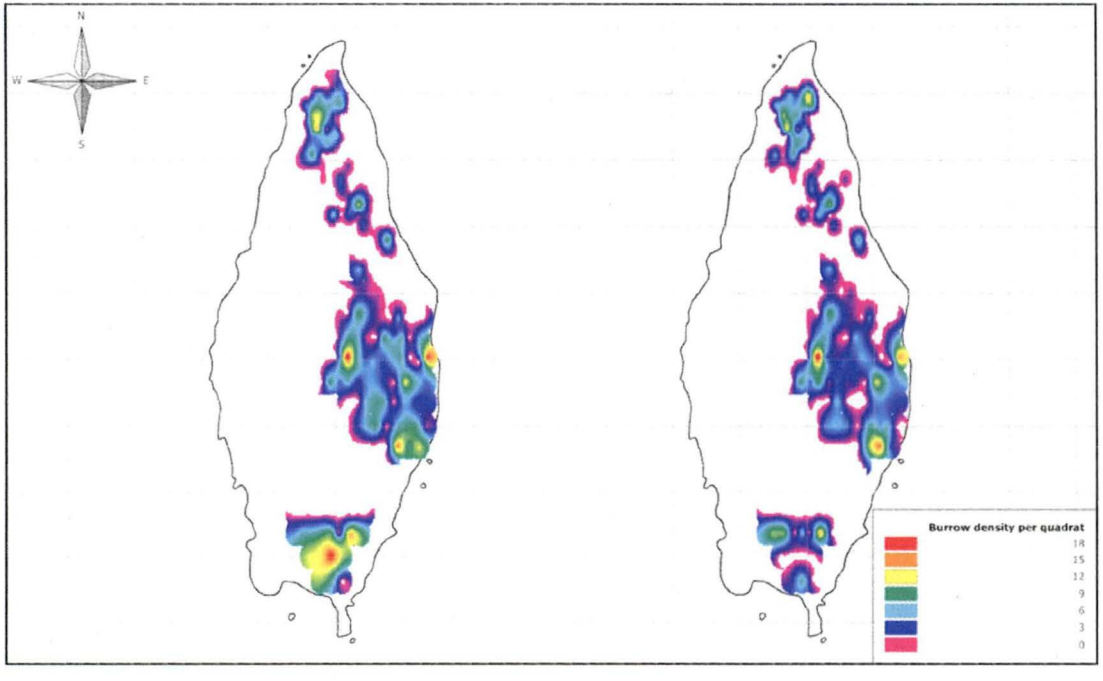

Fig. 2. 5. Burrow density of short-tailed shearwaters in 2005 (left) and 2009 (right), describing the decrease in burrow numbers in the densest part of the colony. Heat colours (reds to orange) have been used to show the highest density of burrows and their distribution over the island with the cooler colours (green to blue) showing areas of lower burrow density.

Discussion

The Wedge Island population of short-tailed shearwaters and little penguins, while representing < 1% of the total numbers of birds of either species, is nonetheless an important study site because there are detailed multi-year counts for both species that can be used to assess changes in population growth rates. The ability to accurately quantify population growth rates is a cornerstone of effective conservation and wildlife management (Caughley & Gunn 1996). Low mortality and reproductive rates of k selected species such as seabirds mean that population declines due to poor reproductive success can take several years to manifest as reduced numbers of breeding adults in colonies. However, any reduction in adult survival, particularly in breeding females can dramatically reduce the number of breeding birds in a colony (Russell 1999; Eberhardt 2002; Oro et al. 2003).

Using data collected over 7 years, we observed two very strong population trends for little penguins and shearwaters: 1) that the short-tailed shearwater population decreased at a rate of 15% per annum and 2) that the little penguin population increased at a very similar rate (17% per annum). While specific vegetation types were preferred by the birds for breeding, these did not alter significantly throughout the 5 years of the study.

Population trends: Short-tailed shearwaters

Successfully diagnosing population declines depends on a series of logical steps (Caughley 1994) including: confirming that the species is in decline, studying the natural history of the species, listing agents of decline, measuring the agents against the species both temporally and spatially and testing hypotheses by experiment to ascertain that the agent is linked to the decline and not merely associated with it (Caughley & Gunn 1996). While isolating the cause of the observed trend is outside the scope of this paper, we discuss possible agents below with the intention of developing and prioritising hypotheses to be further tested.

Onshore effects

As seabirds form natural meta-populations, individual colonies within the complete distribution of the species may form source-sink populations. A 'sink' population occurs when within habitat reproduction is insufficient to balance local mortality but may be sustained by immigration from nearby more productive 'source' populations (Pulliam 1988). Measuring source and sink populations requires intensive effort in marking individuals (Bradley et al. 1991) and a long-term study of short-tailed shearwaters on Fisher Island in Tasmania demonstrated that even marking every individual sighted in the colony within a 44 year time frame was not adequate to assess immigration and emigration rates (Bradley et al. 1991). Recent developments in genetics are allowing the identification of source-sink populations using mitochondrial DNA (mtDNA), and a study on short-tailed shearwaters revealed a surprisingly low level of genetic diversity amongst their distribution indicating a population bottleneck during the last glaciation (10,000 years before present) and a resulting expansion until recent times (Austin et al. 1994).

Local extirpations of short-tailed shearwaters have been observed in other areas in the past, although in all cases they were attributed to habitat encroachment or predation pressure from introduced species such as cats and foxes (Harris & Bode 1981). In our study the population has reduced 63% in five years. The rapidity at which this decline has been observed lends more support to the hypothesis of increased adult mortality or decision not to breed than a decrease in recruitment such as we would expect in a traditional source-sink scenario. However, a reduction in habitat quality may result in a decline in breeding birds.

Whilst the overall density of shearwaters on the Wedge Island colony is historically lower than that in other short-tailed shearwater colonies in Tasmania (Naarding 1980), the relocation of established breeders due to a decline in habitat quality has been observed in other species (eg, Audoin's gull (*Ichthyaetus audouini*), (Oro & Ruxton 2001); common terns (*Sterna hirundo*), (Tims et al. 2004) and kittiwakes (*Rissa spp*), (Danchin et al. 1998; Kildaw et al. 2005)). There are numerous biotic and abiotic factors influencing habitat quality including, but not limited to: ectoparasites, predation, food availability, weather, and interaction between

individuals and these vary both spatially and temporally (Boulinier & Lemel 1996). If the habitat quality in the densest part of the colony has been declining, it may be that established breeders are emigrating to nearby colonies of greater habitat quality which would result in the density dependent decline that we have observed

It should also be recognised however, that while egg laying within the small colony varied between years (Fig. 2.3) without displaying any overall trend, there was also a high error due to the sample size. It is feasible that the sampling density within the smaller colony was not high enough to detect an overall trend (Fig. 2.5), or that this smaller colony, on the northern tip of the island is targeted by new breeders who are elevating the detected numbers of eggs being laid in this habitat. Continued monitoring of the large colony will be required to establish if the current decline reaches equilibrium. While the Fisher Island study would suggest that marking individuals must occur in high numbers to be meaningful, marking of the Wedge Island birds whilst simultaneously monitoring nearby colonies would aid in testing the hypothesis of emigration due to habitat quality decline and also serve to identify if the small colony is being targeted by new breeders.

The practice of culling shearwaters for their meat and feathers for subsistence by indigenous communities has occurred in Tasmania for at least 6,000 years (Anderson 1996), although they have only been commercially exploited since the early 1800's (Skira 1987). All the current harvesting is undertaken on the Bass Strait Islands over a five week season. However, anecdotal evidence suggests that recreational poaching from islands not officially listed as harvest sites is prevalent. Wedge Island is particularly vulnerable to poaching because it is located only 2 km from the holiday destination of Nubeena. In the time that the study has been conducted however, no poaching has occurred on the island, due in large to the presence of researchers on the island during the peak of the harvesting season. Further, the only landing site on the island is on the northern tip (Fig. 2.1) with the remainder of coastline consisting of steep dolerite cliffs up to 90 m in height. Pedestrian access to the largest colony (which is declining) of shearwaters therefore, is treacherous and labour intensive whilst access to the small colony (which is not declining) is just a short walk on stable ground from the

landing site. Therefore it seems that harvesting is unlikely to be the main cause for the current negative population trend.

Whilst the lack of trend in the small colony rules out the influence of poachers, it does perhaps imply that the observed decline may be related to colony characteristics. The effect of onshore habitat characteristics, such as terrain or vegetation type on the reproductive success of short-tailed shearwaters has not been widely studied. However, Bradley et al. (1991) showed that severe weather events resulted in mass chick mortalities, as did Stokes & Boersma (1998) with Magellanic penguins (*Spheniscus magellanicus*) and Kemper et al. (2007) with African Penguins (*Spheniscus demersus*). Severe weather events have negative effects on burrowing seabird colonies in particular because the colonies are fragile due to the tunnelling/burrowing actions of birds. As seabirds are k-selected however, their life history traits tend to buffer them against such episodic variations in breeding success (Pianka 1970).

The position of nests within a colony can affect reproductive success (Schreiber & Burger 2001; Kemper et al. 2007) as can vegetation associations within the habitat. Short-tailed shearwaters were selecting for a preferred vegetation type (1 and 4, Table 2.2) and we observed that the highest rate of decline was occurring in a specific vegetation type (sand and *Poa poiformis*, Table 2.2). However, this was typical of the vegetation type in the densest part of the colony (Fig. 2.6). As there is a preferred vegetation type associated with breeding, we might expect to see a decline in breeding numbers if the vegetation types associated with lower bird densities increased. As the vegetation types themselves did not alter over the duration of the study despite being measured in the first and last reported seasons, we can conclude that the currently observed trend is not being driven by changes in vegetation.

The long-term Fisher Island study reported a decline in the number of breeding birds in the early years of the study (Serventy & Curry 1984; Bradley et al. 1991) which was cautiously attributed to the presence of investigators, although no definitive cause was established (Bradley et al. 1989). During our study, we traversed the colonies whilst conducting the survey at contrasting rates, the small

colony checked seven times per season and the larger colony checked only twice per season. Given that the more intensively checked areas are not displaying any negative trend, in comparison to the less intensively checked areas which are, it may be concluded that the presence of researchers and their activities on the island have not negatively affected the rates of egg laying of shearwaters on Wedge Island. This is in accordance with observations and findings of others on burrow nesting seabirds and particularly short-tailed shearwaters (Saffer et al. 2000; Schultz & Klomp 2000).

Offshore effects

In the past, the at-sea distribution of short-tailed shearwaters has overlapped with a number of major fisheries. By-catch of short-tailed shearwaters between 1952 and 2001 was estimated to have been between 4.1 and 21.2 million individuals (Uhlmann et al. 2005). The worldwide ban on drift-netting reduced the number of incidental catches but short-tailed shearwaters continue to be caught in both inshore driftnet fisheries (Spiridonov & Nikolaeva 2004) and long-line fisheries (Dietrich, Melvin, & Conquest 2008). Consequently, by-catch mortality may decrease populations past a sustainable maintenance point as it contributes to increased adult mortality (Russell 1999; Eberhardt 2002; Oro et al. 2003).

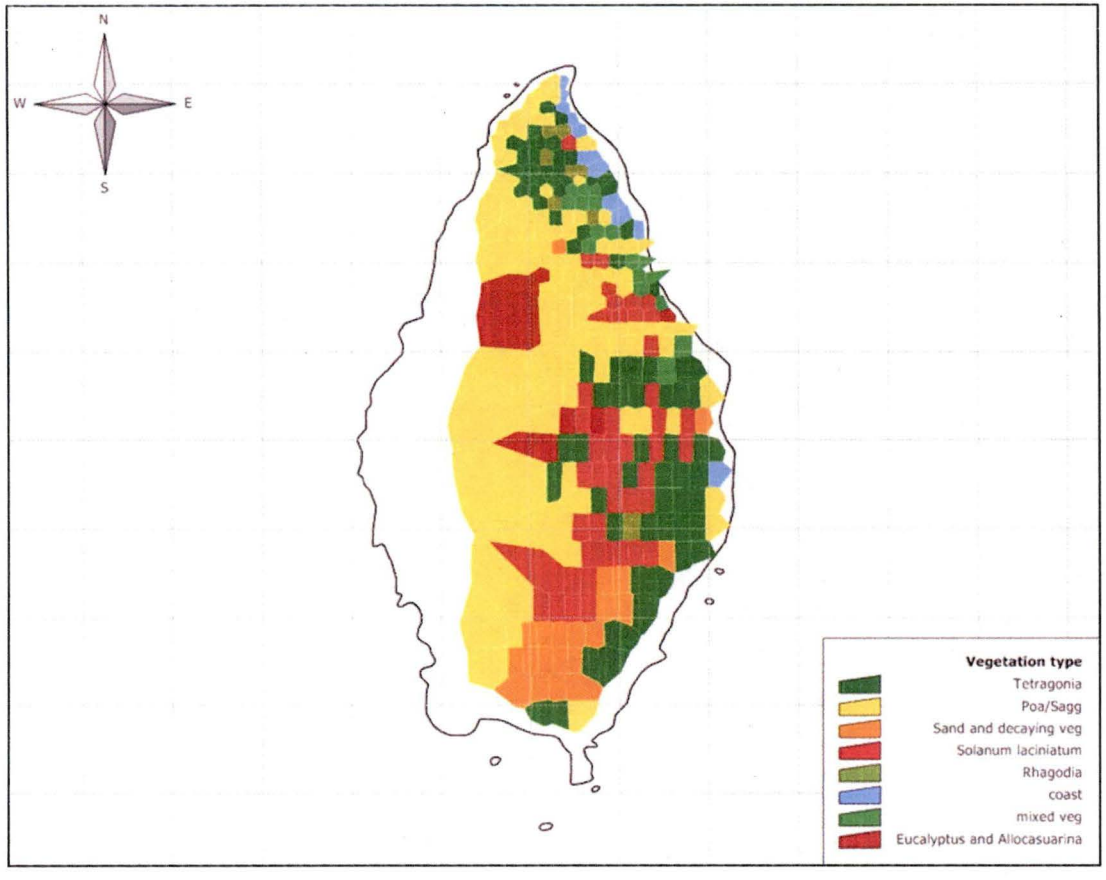

Fig. 2. 6. Vegetation map of Wedge Island showing the distribution of 8 vegetation groups displayed by dominant vegetation (*Eucalyptus* and *Allocasuarina* are grouped together).

Variability in the distribution and abundance of prey is a primary contributor to success in many species of Procellariiformes (Dobson & Jouventin 2007; Nevoux et al. 2007). The northern hemisphere is experiencing rapidly changing environmental conditions at a greater magnitude than elsewhere in the world (Pedersen et al. 2009), which may alter prey location distribution and prey quality. While these changes may not affect breeding success (i.e. chicks fledged from eggs laid) they determine the amount of resources birds can accumulate and store for their long (15 000 km) inter-hemispheric migrations south. As short-tailed shearwaters migrate from the Bering Sea, their body condition on arriving in the breeding colonies may determine whether they breed. Also, if there is mortality during the winter season, fewer birds will return at the start of the season. A second opportunity to replenish body condition occurs on the 'honeymoon' trip to Antarctic waters between arrival in the breeding colonies in September and the start of egg-laying in November (Weimerskirch & Cherel, 1998). Currently the breeding population has been estimated from a count of breeding birds in December after eggs have been laid; however, this is not measuring the return rate to the colony post migration. A simple method of testing return rate in order to separate reduction in numbers originating in the northern hemisphere and that from the south will be to take a population census in September when the birds return from the winter migration in order to determine if levels are similar to those recorded in December.

Perhaps the greatest impediment to understanding the causes of the decline in this colony is the lack of comparable data from elsewhere in the species distribution. It is possible that this decline may be a local phenomenon; however, there are many historical precedents for rapid decline in previously common species (eg. Passenger pigeons (*Ectopistes migratorius*) (Schorger 1955), North American bison (*Bison bison*) (Isenberg 2000), African elephant (*Loxodonta sp.*) (Blanc et al. 2003), Atlantic cod (*Gadus morhua*) (Jackson et al. 2001). The sooty shearwater (*Puffinus griseus*) which breeds in New Zealand and occupies a similar trophic niche with overlapping foraging range as the short-tailed shearwater is also reported to be declining (Scott et al, 2008). Any change in population size of upper trophic consumers that integrate environmental variability over large regions of the

oceans can theoretically provide evidence of large scale changes (Hindell et al. 2003).

Population trends: Little Penguins

In contrast to our observation that little penguins are increasing in numbers on Wedge Island, populations of Little Penguins have been declining elsewhere in south eastern Tasmania (Stevenson & Woehler 2007), particularly on the mainland where penguins are subject to a number of anthropogenic factors including: habitat encroachment, human disturbance at nesting colonies and predation from feral and domestic animals. There are many offshore islands including Wedge Island, where small populations of penguins exist without the pressures experienced by those on the mainland; however, no data are available on population trends from these islands.

The most likely explanation for the increasing number of penguins on Wedge Island is that the island was home to a small population of feral cats prior to their removal in 2003. Little penguins are present on Wedge Island for the entire year as opposed to the shearwaters which are present from September to April only. As the island supports no mammals, the penguins become an important part of the diet of cats particularly during the winter months, although even in summer when shearwaters were present, the cats were preferentially preying on the penguins (Smith 2003). With their removal, the little penguins on Wedge Island are under reduced predation pressure on land and subsequently breeding numbers have improved.

Little penguins and short-tailed shearwaters breed sympatrically on Wedge Island which may have resulted in a reduction in inter-specific competition for nest spaces as the numbers of shearwaters on the island have declined. However, the level of burrow occupancy of short-tailed shearwaters on the island (0.2 burrows m^2 at the start of surveying in 2003) is significantly lower than many other shearwater colonies around Tasmania which range from a density of 0.3 burrows m^2 to 1.04 burrows m^2 (Naarding 1980). Little penguins have been observed in many other shearwater colonies with higher density of birds, and if nest space were at a

premium we would expect to see higher occupancy rates of both species across the island.

Conclusions

Having excluded recreational muttonbirding, investigator disturbance and onshore effects as contributing to the decline of short-tailed shearwaters on Wedge Island, we are left with four testable hypotheses in the form of source-sink population dynamics, emigration due to a decline in habitat quality, incidental by-catch and offshore environmental variation. Source-sink population dynamics will be difficult to test as they generally require long-term studies of marked individuals. However mtDNA sampling is currently being undertaken on Wedge Island and neighbouring colonies in order to try and identify possible source-sink populations. Emigration, like source-sink is difficult to test, requiring long-term studies of marked individuals and studies of neighbouring colonies. Incidental by-catch is also difficult to test and would involve the collection of genetic material at the by-catch sites and also from all nearby breeding colonies so that the bird's colony of origin could be determined. Individual genetic testing is difficult because breeding and feeding locations can be very distant (Baduini et al. 2006; Cherel et al. 2006) and obtaining samples from by-catch sites can be challenging.

Given the overall trends for Procellariiformes in the Southern Ocean, the trends for the related sooty shearwaters in New Zealand and the time scale in which the decline has occurred, it is likely that the population trends are being driven by offshore environmental effects (Table 2.3). The effects of environmental variation are testable via collection of oceanographic data that is temporally and spatially relevant to the Wedge Island population. Whilst the causes for changes in population trends are often subtle, complex, multifaceted and difficult to test, detecting population changes can act as a spur for directed, hypothesis driven studies. Thus continued monitoring of this population and others in the south east of Tasmania is prudent for understanding the continuing population trends of short-tailed shearwaters.

Table 2. 3. A summary of the possible contributors to the decline in short-tailed shearwaters on Wedge Island. Two of the possible causes are difficult to test. However, the most likely explanation is that the recorded decline is due to offshore environmental changes.

Hypothesis	Assessment	Testability	How?
Source-sink population dynamics	unlikely but failed to discount	yes	requires genetic studies of populations + long time series
Emigration due to habitat quality decline	possible but difficult to test	yes	requires marking and studies of nearby habitats
Recreational muttonbirding	discounted	N/A	N/A
By-catch and fisheries competition	possible but difficult to test	yes	requires genetic studies of bird-bycatch
Investigator disturbance	discounted	N/A	N/A
Onshore effects (habitat characteristics)	discounted	N/A	N/A
Offshore effects (oceanographic variability)	plausible	yes	requires long-term modeling based on environmental variable

Acknowledgements

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Chapter 3

Investigator disturbance in short-tailed shearwaters (*Puffinus tenuirostris*) and little penguins (*Eudyptula minor*)

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Abstract

Field-based animal researchers need to balance the potential adverse effects of their research activities against the benefits of research outcomes, but the data required to do this are often lacking. Assessing, and subsequently reporting the effects of researcher activities on wild animal populations can be difficult, so that studies to detect these effects sometimes lack rigour or fail to encompass sufficient time to ensure that the effects are tested under a range of environmental stresses. We monitored the effect of investigators working in colonies of two seabirds, the short-tailed shearwater (*Puffinus tenuirostris*) and the little penguin (*Eudyptula minor*). Disturbance of breeding birds while checking nests or the weighing of chicks to monitor growth are very common activities for demographic and ecological studies, but how these activities may influence the birds is rarely measured. We investigated differing levels of disturbance during both activities over five years to assess their effect on egg laying, chick survival and growth rate and observed no effect for nest checking or handling of short-tailed shearwaters and indeterminate effects for handling in little penguins. Over a period of several years the study has observed a large scale decline in the number of breeding shearwaters and includes years when control nests had above and below average breeding success.

Introduction

There is an increasing need for studies involving field work in natural ecosystems to monitor the effects of the researcher on the subjects (Dalton 2005, 2006; McMahon et al. 2006; Wilson & McMahon 2006; McMahon et al. 2008). There are two reasons for this. The first is to ensure the integrity of results *i.e.* to establish that the research methods are not altering or biasing the collected data. The second is to be conscious of the ethical implications of the work on the animals and ecosystems (Minteer & Collins 2008) which is a central tenet of research and ordinarily taken into consideration when designing experiments. Despite the need for quantitative studies, relatively little has been published on the effects research may be having on wild animals (Wilson & McMahon 2006). The paucity of such studies is problematic for non-scientific stakeholders (*e.g.* ethics committees and management authorities) and can culminate in decisions based on a subjective and/or cautionary approach rather than an objective, evidence-based approach (Green & Bradshaw 2004; Dalton 2006; Wilson & McMahon 2006).

One effective approach is for field researchers to include monitoring research effects as a component of their overall research program. In particular, the type of direct effects arising from a particular study, the acceptable level of effect and the potential impacts on the larger population all need to be considered in the research design. Equally important is the need for multi-year studies to accommodate the likelihood of differing levels of response in times of differing environmental stress when effects of the investigator could be aggravated (McMahon et al. 2008). At present, few studies incorporate all of these features.

Our study on the responses of two sympatric breeding seabird species (the short-tailed shearwater *Puffinus tenuirostris* and the little penguin *Eudyptula minor*) to environmental conditions was designed to include a monitoring component so that we could test for any confounding effect of investigator disturbance. The short-tailed shearwater (*Puffinus tenuirostris*) is one of the most numerous seabird species in the world with approximately 23 million birds breeding in Australia each year (Skira 1991). They migrate annually from their breeding colonies in southern Australia to winter feeding grounds in the Bering

Sea. Their current population on Wedge Island (Tasmania, Australia) has declined from 36 569 ± 7291 to 12 602 ± 1697 breeding pairs between 2003 and 2010 (Chapter 2) representing a loss in the order of 6848 birds per year.

Breeding sympatrically with the short-tailed shearwater on many offshore islands in Tasmania is the little penguin (*Eudyptula minor*). The global population of little penguins is between 350–600 000 breeding pairs (Marchant et al. 1990) with 1020 ± 228 breeding pairs present on Wedge Island (Chapter 2). The use of sympatric species allows us to monitor multiple trophic levels (as the main prey is different for both species) and multiple spatial scales as penguins are constrained to feeding within approx 200 km of their breeding site, whereas shearwaters may travel as far as Antarctica to obtain food (Weimerskirch & Cherel 1998).

It has been postulated that animals respond to humans as they would to potential predators (Frid & Dill 2002; Beale & Monaghan 2004). As such, burrowing seabirds (*e.g.* shearwaters and little penguins) are likely to respond aggressively (stressfully) when researchers are working in a burrow where their genetic investment (the chicks) resides. The common activities researchers perform are nest-checking for presence or absence of adults, eggs and chicks, and capture of birds for measurements such as weighing. Disturbances of this nature to nests and birds can result in decreased nest site fidelity in some burrowing species (Blackmer et al. 2004). Disturbance effects may be exacerbated by secondary effects such as nesting density (deVilliers 2008) which is important as overall declines will result from density dependence rather than direct disturbance (Gill 2007). Moreover, substrates in colonies burrowing species are often fragile and unstable due to bio-perturbation; investigator damage can occur by partial or total collapse of a burrow while investigators are navigating through the colony or are checking burrows.

Our primary aims in this study were to quantify the effect of investigator disturbance on three key life history traits – rate of egg laying, survival, and growth of chicks of short-tailed shearwaters and little penguins at two common low levels of investigator disturbance (nest checking and handling) over multiple years. Specifically we hypothesise no short-term effects on those life-

history traits. However, long-term effects are less certain. In this study we aim to provide information: 1) relevant to future seabird research planning, 2) that can be incorporated into our primary research on changes in the marine environment and 3) contribute to the broader debate on animal welfare in wildlife research.

Methods

Field work was undertaken on Wedge Island in south-east Tasmania, Australia (43° 07' S, 147° 40' E) on short-tailed shearwaters (STSW) and little penguins (LP) during October-April 2002–03, 2004–05, 2005–06, 2006–07, 2007–08 and 2008–09. All seasons will subsequently be referred to by their finishing year, *e.g.* 2002–03 is referred to as the 2003 season.

Four levels of investigator disturbance were tested (two levels of nest checking and two levels of handling) for each species, lower and higher levels of disturbance within each activity are regarded as 'controls' and 'treatments' respectively, the details of which are expanded on below.

Researcher activity 1: Nest checking

The island (length 1.6 km× 0.8 km – at its widest point) was divided into 35 east/west line transects (length 40 –450 m). A stratified sampling regime was used such that, transects 1–20 which were in the area of highest little penguin density were 25 m apart, and transects 21–35 in low penguin density areas were placed 50 m apart. Circular sampling units (quadrats) were placed at 20m intervals on transects 1–20 and at 25 m intervals on transects 21–35. All burrows within a 2 m radius of the sampling unit centre were individually marked using flag markers (plastic tabs mounted on wire staves). A total of 674 shearwater burrows were marked in 241 quadrats in this way during the 2004 season; of these 473 burrows (transects 17–35) were checked twice to monitor survival of chicks (once in December to establish laying success and once in April to establish fledging success) and the remaining 201 burrows (transects 1–16) were checked monthly for a total of seven times. Burrows were checked during daylight hours between sunrise and sunset. Transects 1–16 were chosen for the intensively checked area due to the smaller colony size and stable substrate of this area's perimeter which allowed for access without frequently traversing unstable areas. Burrow contents were observed without handling animals by using a custom made 'burrow scope' (a lipstick camera with infra-red (IR) lights attached to a 3 m flexible tube and wired to a 3.5 inch colour monitor). Burrows checked seven times over a season constituted the 'test' treatment and burrows checked twice a season the 'control' treatment. While the control burrows were checked twice per season, the individual birds

were disturbed only once (incubating adults in December and nearly fledged chicks in April). We recognise that a true control would involve no disturbance, however due to the nature of the study and the method of data collection, this was not possible. We also categorised quadrats as either stable or unstable based on the fragility of the burrows and the surrounding substrate. A quadrat was considered unstable if there was soil movement of the burrow roof in greater than 2 burrows, and otherwise stable. Little penguins were not included in this analysis due to their breeding asynchrony and low numbers in the sampled area.

Differences in the numbers of STSW eggs laid among years were examined to ascertain any on-going effect on nest site fidelity. Negative effects might include the detection of decreasing numbers of eggs being laid each year, particularly in the intensively checked areas.

Researcher activity 2: Chick handling

Short-tailed shearwater burrows (n = 50) were randomly assigned to either a control group (n = 25) or a test group (n = 25). Chicks were removed from burrows and weighed in a cloth bag using a 1 or 2 kg Salter® spring balance whereas head length (from the tip of the beak to the occipital condyle), beak length (from the tip of the beak to the base where the feathers begin), beak width and beak depth (from just behind the nares) were measured to within ± 0.05 mm with Vernier callipers. Handling time (from extraction from the burrow to return) averaged approximately 3 minutes and was constant for the duration of the study.

Permitting constraints allowed us the use of 50 chicks of each species as opposed to 50 nests, therefore little penguin burrows used for chick growth rate measurements varied in number due to the uneven number of eggs laid by individual parents. Consequently, to weigh 50 penguin chicks, 22, 29 and 27 little penguin burrows (years 2003, 2005 and 2006 respectively) were selected. These chicks were weighed and measured using the same techniques as the shearwater chicks with analogous handling times. Control chicks for each species were weighed once on their initial capture and again prior to fledging.

Test chicks were weighed an additional two times for a total of four measurements throughout development. For little penguins years 2007 and 2008 were excluded from the analysis due to extreme breeding asynchrony resulting in only control level handling for these two years.

Statistical Analysis

Researcher activity level 1: Nest checking - (short-tailed shearwaters only)

While it is likely that environmental factors such as year and habitat stability will affect fledging and rates of egg laying, for this study we were primarily interested in the effect of the investigator. The stability parameter was included as it occurred irrespective of transect location and provided a correction factor for any effects resulting from the non-random sampling regime that was employed to reduce any effects of frequently traversing unstable areas (see methods, researcher activity 1: Nest checking).

We compared these two levels of disturbance using generalized linear models (GLM) in the R statistical program (R Development Core Team 2009). The model fixed terms were continuous: *fledge* (the number of fledged birds per quadrat), *eggs* (the number of eggs laid per quadrat) and *year* (2003, 2005, 2006, 2007, 2008, 2009, 2010). There were also two binary terms: *treatment* (1 = control, 2 = treatment, n = 201 and 473 respectively) and *stability* (1 = unstable, 0 = stable). The number of birds fledged was used as the response variable and models were built to test both additive and interaction terms. Each model was constructed using a Poisson error distribution and a log link function as examination of the residuals revealed these to be the most appropriate.

Bayesian Information criteria (BIC and ΔBIC) scores were used to rank models and determine the most parsimonious model as they provide greater strength when the sample size is large and contains a small number of variables with potentially large effects (Burnham & Anderson 2004). Generally, ΔBIC values of: 1) < 2 implying that the models have substantial support, 2) $2 <$ ΔBIC < 7 showing some support and 3) ΔBIC > 7 showing no support for that model (Burnham & Anderson 2001).

As short-tailed shearwaters exhibit a high degree of nest site fidelity and the same burrows were checked every year (with the exclusion of 2003), it is likely that the same breeding pairs are being disturbed every year. Consequently, if investigator effects are cumulative over time we might expect to detect a decrease in the number of eggs laid per quadrat in the areas with a higher rate of disturbance. Mean number of eggs laid per quadrat were compared using the same GLM approach as for fledging rates.

Researcher activity level 2: Chick handling – (short-tailed shearwaters and little penguins)

Survival (n = 50, n = 50, n = 50, n = 47) and fledging mass of surviving shearwater chicks (n = 25, 28, 36 and 30) were compared using a 2-way ANOVA between treatment and year, and little penguin fledging mass was compared across groups using the same GLM as for researcher activity level 1 with corrected Akaike's information criterion (AICc and ΔAICc) scores used to rank models in this case due to the smaller sample sizes. The GLM was used for the little penguin analysis as most breeding pairs of little penguins lay two eggs and often raise two chicks, and therefore comparing fledging weight between chicks using ANOVA would result in pseudo-replication. Survival for handled little penguins was not calculated due to the infrequency of sampling meaning we could not determine with certainty if a chick had died between visits or had fledged prior to us returning and therefore we also interpret the mass comparison results with some caution recognising that there will be low power associated with this analysis. Fledging mass of little penguins was expressed as mean surviving fledging mass per burrow (n = 14, 16, 13).

Results

Researcher activity level 1: Nest checking - (short-tailed shearwaters)

None of the models were particularly good at explaining fledging success (fledge) with the best ranked model explaining only 12.02% of the data variability (percent deviance). The model with the strongest support was fledge~stability+year (Table 3.1) indicating that the number of chicks fledged was affected most strongly by the stability of the quadrat and the year of the

study. This indicates that there were years of relatively poor performance when the effect of the investigator might have been exacerbated (Fig. 3.1a). However, there was little support for a disturbance effect during nest checking in any year of the study with the nest checking parameter actually ranked beneath the null model according to the ΔBIC values (Table 3.1).

Table 3.1. Model Bayesian Information Criterion (BIC), ΔBIC, wBIC and percentage deviance weights for short-tailed shearwater chicks fledged and eggs laid per quadrat across year, quadrat stability and nest checking.

model	BIC	dBIC	wBIC	pcdev
fledge~stability+year	1746	0	0.9549	12.03
fledge~checking+stability+year	1752.1	6.11	0.0451	12.05
fledge~year	1771.1	25.05	0	8.03
fledge~year*stability	1771.7	25.67	0	12.72
fledge~stability	1776 2	30 18	0	4.19
fledge~checking+year	1776.7	30.73	0	8 1
egg~stability+year	686.2	0	0.4922	17
egg~checking+stability+year	686.3	0.16	0.4538	19.09
egg~year*stability	691.2	5.07	0.0389	17
egg~year*checking*stability	693.3	7.14	0.0138	24.77
egg~year	698.6	12.41	0.001	9 56
egg~checking+year	701.9	15.72	0.0002	10.31

Egg laying

Again, the best model, explaining 15.8% of the deviance did not include the disturbance term, with the most strongly supported model being *egg~stability + year*. There was some low level support for the inclusion of the disturbance term (*egg~ treatment + stability + year,* ΔBIC = 4.14, % deviance = 16.05, Table 3.1). While this may indicate a disturbance effect, analysis of the model coefficients show that there were only a lower number of eggs laid in the intensively checked area in 2006 (estimate = -0.50 ± 0.17, p = 0.003). Fledging success for 2006 in the more intensively checked area was not significantly lower than in any other year and the effect has not been observed since that year. Given the trend for reduced numbers of eggs being laid across the entire colony (Fig. 3.1b), it is likely that the lower rate of egg laying in 2006 was not due to the investigator, but is due to an effect not analysed by the current study.

Researcher activity level 2: Chick handling

Survival of handled shearwater chicks was related to the level of handling ($F_{3,204} = 2.97$, $p = 0.034$), but this also varied among years (year*handling $p = 0.03$) and this result is largely driven by the low survival of control chicks (*i.e.* those only handled once) in a single year (2003). As handling did not produce a significant result for subsequent years ($F_{3,154} = 1.05$, $p = 0.3$) it seems unlikely that in 2003 handling produced higher survival and this result may be due to an effect not currently analysed in this study (Fig. 3.2).

Fledging mass of short-tailed shearwaters showed no significant difference in either intensity of handling or among years (($F_{3,114} = 2.255$, $p = 0.086$) year*handling $p>0.1$, year $p> 0.1$, treatment $p>0.1$) (Fig. 3.3). For penguin fledging mass, there was virtually no difference in support between the first three models (ΔAICc>2), *mass~year * treatment*, *mass~year + treatment*, *mass~year* (Table 3.2) which may suggest an effect of handling on the fledging mass of little penguin chicks in certain years. On examination of the coefficients, only in 2005 did birds handled four times fledge at a lower mass than those handled twice (coefficient estimate = -203.09 $\pm$ 89.25, $p = 0.02$), however in 2003 and 2006, the reverse was true (Fig. 3.3). Given the low power of this analysis, a greater sample size would be needed to ascertain if handling four times during a season is having a negative or positive effect on fledging mass or if this an artefact of the low sample size. The model set showed no support for the effect of treatment on its own (*mass~treatment* (ΔAICc = 7.08, pcdev = 6.5, Table 3.2) and overall fledging mass was not lower than average in the year that resulted in a slightly lower fledging mass for handled birds.

Table 3.2. Model corrected Akaike's Information criterion (AICc), ΔAIC, wAIC and percentage deviance weights for little penguin fledging mass for year and level of handling (twice vs four times per season).

model	AICc	dAICc	wAIC	pcdev
mass~year*handling	804.7	0.00	0.3821	28.67
mass~year+handling	805.1	0 39	0.3137	22.18
mass~year	805 2	0.56	0.2890	18.93
mass~handling	811.7	7.08	0.0111	6.55
mass~1	813.7	9.07	0.0041	0.00

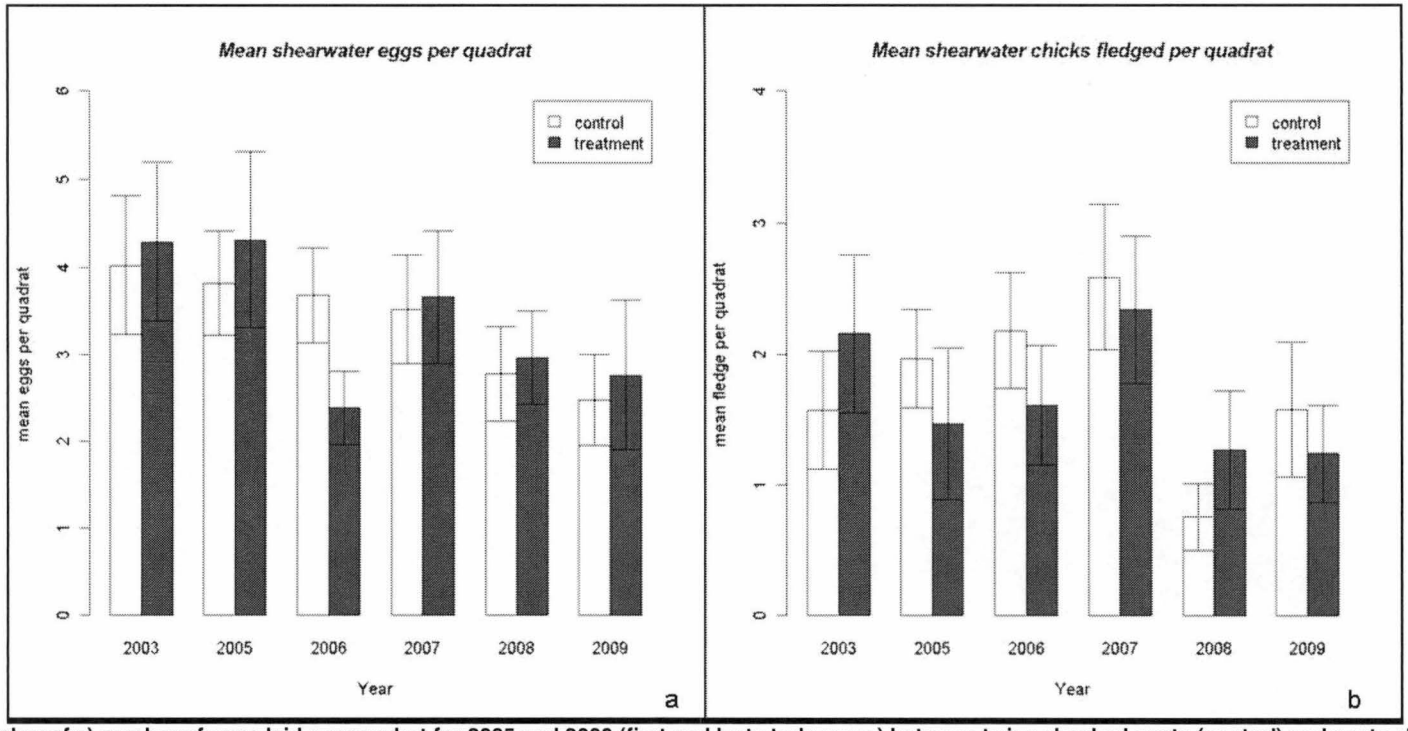

Fig. 3. 1. Mean number of a) number of eggs laid per quadrat for 2005 and 2008 (first and last study years) between twice checked nests (control) and nests checked seven times (treatment)); and b) short-tailed shearwater chicks fledged per quadrat for a five year data set comparing nest checks twice per season (control) and nest checks seven times per season (treatment). The error bars represent the 95% confidence intervals.

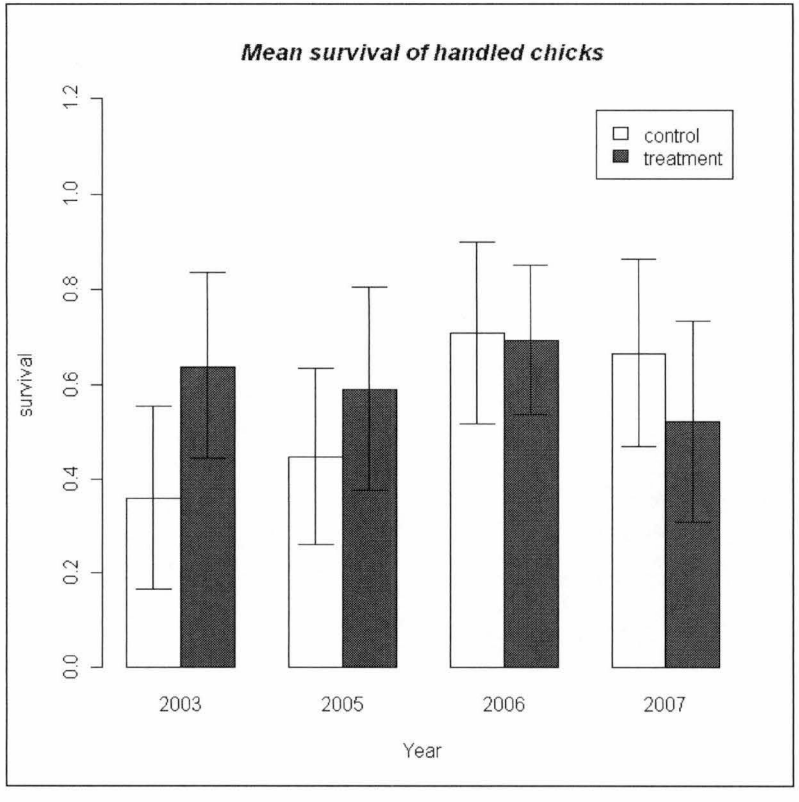

Fig. 3. 2. Mean survival of handled shearwater chicks from 2003–07 (n = 50, n = 50, n = 50, n = 47) of short-tailed shearwater chicks between birds handled twice (control) and birds handled four times (treatment). The error bars represent the 95% confidence intervals.

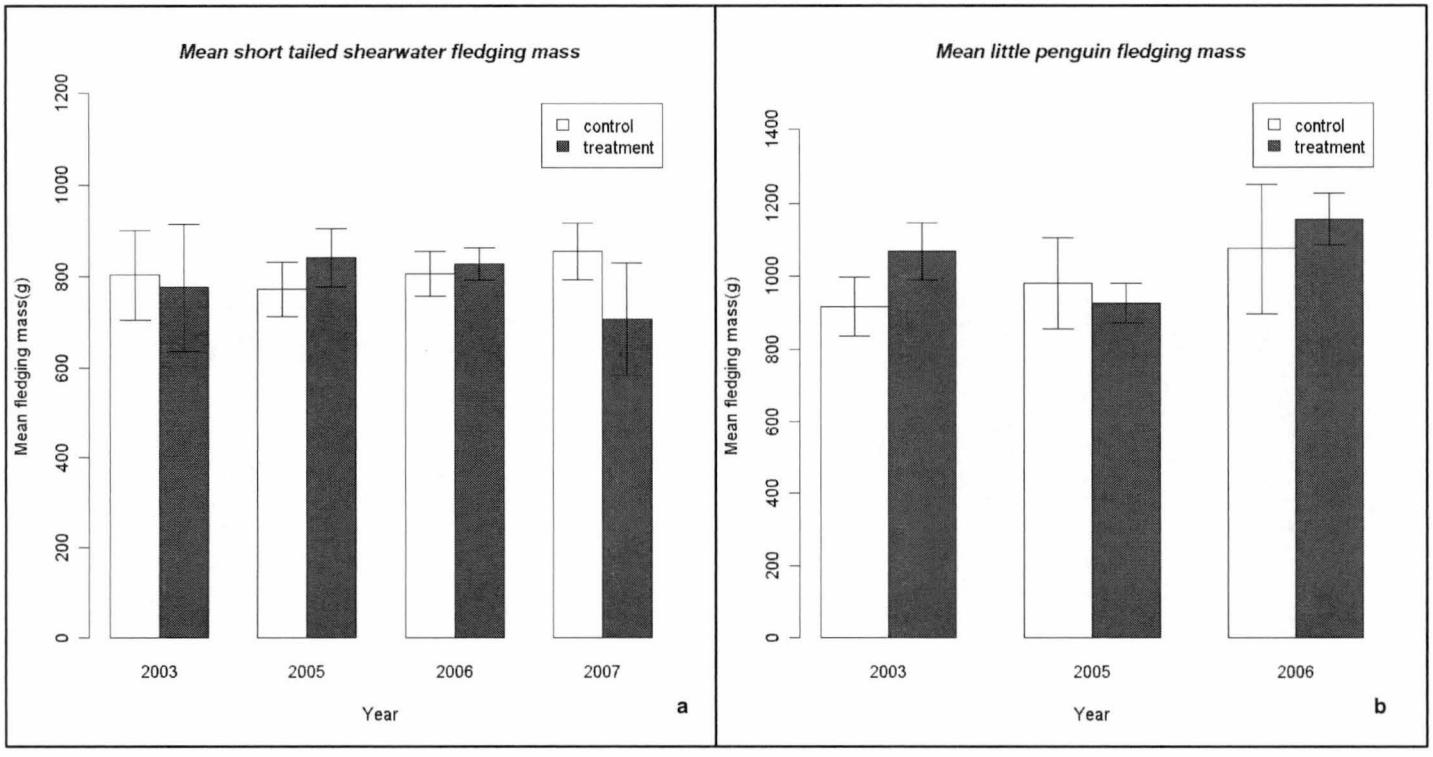

Fig. 3. 3. The fledging masses of a) short-tailed shearwaters from 2003–07 (n = 25, n = 28 and n = 36 respectively) between birds handled twice (control) and birds handled four times (treatment – clear). The error bars represent the 95% confidence intervals; and b) The fledging masses of little penguins from 2003–06 (n = 24, n = 21 and n = 18 respectively) between light handling (control – clear) and more intense handling (treatment – shaded). The error bars represent the 95% confidence intervals.

Discussion

All studies that involve researchers interacting with wild populations of animals should quantify the effects of their activities. Any negative effects need to be considered with respect to the relative importance of the study, for the overall well being of the population or species, and with respect to the resulting integrity of the data themselves. In our case, we wanted to quantify the effects of environmental stochasticity on life history parameters but to effectively interpret our results we needed firstly to know of any confounding effects due to our research activities. Equally important, these effects (or lack thereof) need to be reported, to help informed scientific and management decisions for future studies (Wilson & McMahon 2006).

We have demonstrated that, despite researchers being regularly present in a large seabird colony throughout the breeding season, there were no detectable negative effects of research activities on three key life-history parameters; egg laying, survival of chicks and fledging mass in short-tailed shearwaters although there may be a variable effect on fledging mass in little penguins. While the levels of disturbance for adult birds were low even at the 'test' level, the observations were consistent over the entire five years of study, which included years of reduced egg laying and fledging of chicks. This is an important finding as it shows that even when environmental conditions are poor and researcher effects would be exacerbated, we were unable to observe any negative effects of the research activities on short-tailed shearwaters.

While these results were clear for the short-tailed shearwaters, the results for the little penguins were less so. We detected inconsistent effects in the fledging masses of little penguins that are biologically difficult to interpret. The key reason for this is twofold. The sample size was not high enough and the rate of sampling was inadequate. For a species like the short-tailed shearwater that exhibits synchronous breeding, the sampling regime employed provided enough power to draw conclusions on the effect of investigators. However, the breeding asynchrony of little penguins meant that four weekly checks were not adequate to accurately establish fledging rates or obtain enough points to calculate growth

curves and the sample sizes of 50 chicks (rather than 50 nests) resulted in pseudo-replication of the data for analyses.

We cannot conclude that we had either a positive or negative effect on the fledging mass of little penguins however in order to confirm or refute our findings, the sampling rate would need to be higher and more frequent which would potentially impact negatively on the survival or fledging mass of the studied animals. It is perhaps this quandary that results in the under testing and/or reporting of investigator effects on wild animal populations. Effects can be subtle and difficult to interpret as we have shown here. When any study is being designed it is important to consider the research questions, the desired outcome, and then model the study on the minimum impact needed to answer them.

In previous studies (Table 3.3), the effects of researcher activity on vital rates such as breeding success and growth vary according to the species studied, habitat characteristics and the intensity of disturbance. For example, surface nesting seabirds seem to be far more prone to researcher effects with 7 out of 13 reported procedures resulting in some kind of significant effect on survival and/or growth. These activities ranged in intensity from daily walking of transects (jackass penguin, (Burnham & Anderson 2001)) to daily nest checks (black legged kittiwake, (Sandvik & Barrett 2001)) to daily weighing and measuring (black skimmer, (Safina & Burger 1983) and attachment of platform transmitter terminals on Adélie penguins (Ballard et al. 2001).

However, inter-study comparisons need to be approached and interpreted cautiously due to the varying intensity and nature of the research activity. For example, Hull & Wilson (1996) observed no investigator effect on two species of surface nesting penguins (royal and rockhopper), despite daily visitation to the colonies whilst Hockey and Hallinan (1981) observed significant effects of investigators in jackass penguins with a similar rate of disturbance. Most investigator effects vary within and between species and therefore should be assessed on a case by case basis (Casper 2009). Indeed, a recent review on human disturbance (both from tourism and research) in Antarctica by deVilliers (2008) also details species specific responses to varying intensities of disturbance.

However, it could be argued that even those species that have exhibited an investigator effect may find that effect greatly reduced or negated by modifying the sampling regime whilst still maintaining data integrity and usefulness.

While caution is needed when extrapolating from observations such as ours to other species, some generalities are warranted especially given the consistency of the results over a number of years for short-tailed shearwaters. We would suggest that our sampling regime could provide a baseline for other burrowing seabird species in which sampling effort resulting in minimal disturbance with no discernable impact on growth rates or survival is still contributing useful data.

Overall, burrowing seabirds seem to be less susceptible to the effects of research activity than surface nesting seabirds. Only two of the nine studies on burrowing seabirds reported an effect on growth, reproductive success, or nest site fidelity. A study of Atlantic puffins, which had a control level of disturbance that far exceeded our treatment level Rodway et al. (1996) found a 38% reduction in chick productivity which was persistent for one year following the conclusion of the study. In a study of Leach's storm petrel (Blackmer et al. 2004) with disturbance levels similar to those in our study, the researchers recorded a decrease in hatching success in birds checked daily and weekly compared to those checked only once during incubation and once after hatching. However, previous work on short-tailed shearwaters (Saffer et al. 2000) in which birds were weighed twice a day for 84 days (136 handling events) recorded no differences in fledging weights compared to those that were weighed and measured only once. There may be many habitat related factors other than human disturbance that may affect reproductive performance of seabirds which include the stability of the substrate in which the birds are breeding, densities in colonies, and colony exposure.

Table 3.3. Summary of investigator disturbance studies (either published autonomously or as part of a general study) showing species, nesting habit, researcher activities undertaken during the study, recorded effects and whether or not the effect was due to the investigator.

Species	Nesting habit	Action	Growth or survival effect	Investigator effect
Atlantic puffins[1] *Fratercula arctica*	Burrowing	Weighing and measuring once during incubation, every 4 days prior to hatching and up to pre-fledging then every two days until fledging VS late	Yes	Yes

		in nestling then every two days until fledging 2 year duration		
Burrowing Owl[2] *Athene cunicularia*	Burrowing	Attachment of radio transmitters and leg bands VS leg bands – testing on natal recruitment and fledging	No	No
Cory's shearwater[3] *Calonectris diomedea*	Burrowing	Weighing and measuring at 4hr intervals for three days VS once per day VS once at start and end	No	No
Hutton's shearwater[4] *Puffinus huttoni*	Burrowing	Burrows checked through inspection hatched every second day prior to laying then every day for 4-10 days after laying, chicks weighed and measured every second day until fledging VS burrows checked three times through inspection hatches VS burrows checked three times with burrowscope	No	No
Leach's storm petrel[5] *Oceanodroma leucorhoa*	Burrowing	Both parents weighed, banded (once), measured each day until fate of egg determined VS same procedures once a week VS visited once during incubation and once to determine hatching success. Burrows checked following year to determine ongoing effects	Yes	Yes
North Island little shearwater[6] *Puffinus assimilis haurakiensis*	Burrowing	Adults weighed every second day while incubating and chicks weighed daily after hatching	No	No
Short-tailed shearwater[7,8] *Puffinus tenuirostris*	Burrowing	Weighing and measuring at 4hr intervals for five nights over three periods and two years (120 measurements) VS weighed once. Weighing twice a day for 84 days, measured every 16 days (136 handles) VS 18-20 handlings over 84 days VS one weigh and measure	No Yes	No No
Wedge-tailed shearwater[7] *Puffinus pacificus*	Burrowing	Weighing twice a day for 84 days, measured every 16 days (136 handles) VS 18-20 handlings over 84 days VS one weigh and measure	No	No
Adelie penguin[9] *Pygoscelis adeliae*	Surface nesting	3 seasons, radio transmitters (RT) attached with signal monitored from a distance VS flipper bands and PIT tags, monitored via weighbridge VS time depth recorder and RT attachment with all undergoing daily nest checks Stomach lavage Platform transmitter terminal (wt 170g, area 800mm^2) attachment TDR attachment (wt 50g, area 520mm^2) attachment	No No Yes No	No No Yes No
Black-browed[18]	Surface	Blood sampling, handling time <5minutes, 1 bird	No	No

Albatross *Thalassarche melanophris*	nesting	per nest VS no handling or blood sampling Distance marked then 9 birds blood sampled prior to foraging VS 7 not sampled	No	No
Black guillemots[10] *Cephus grillile*	Surface nesting	Nest checks (including diameter, depth, particle size, overall shelter, density and distance from neighbour) daily VS nest checks every 4 days	Yes	Yes
Black legged kittiwake[11] *Ryssa trydactyla*	Surface nesting	Daily nest checks, cross-fostering, weighing of chicks twice and weighing of adults twice VS nests checked once with chicks weighed, measured or counted	Yes (nest attendance) No (chick growth)	Yes
Black skimmer[12] *Rynchops niger*	Surface nesting	Weighing and measuring daily VS weekly until hatching and then daily VS weekly	Yes	Yes
Eurasian oystercatcher[13] *Haematopus ostralegus*	Surface nesting	Nest checking three times daily for four days Vs once every other day	No	No
Jackass penguin[14] *Spheniscus demersus*	Surface nesting	One transect walked daily for 7 days VS one transect walked 2 hourly for 2 days VS one transect walked hourly for two days	Yes	Yes
Rockhopper penguin[15] *Eudyptes crysocome*	Surface nesting	Traversing transect plus handling of chicks and adults twice weekly VS no handling or traversing	No	No
Royal penguin[15] *Eudyptes schlegeli*	Surface nesting	Traversing transect plus handling of chicks and adults twice weekly VS no handling or traversing	No	No
Southern Giant Petrel[20] *Macronectus giganteus*	Surface nesting	Intensive banding program at three colonies	Yes	Yes
Wandering[19] Albatross *Dimodea exulans*	Surface nesting	Visual checks twice in three days VS four times in one day VS twice daily for three consecutive days	Yes	Yes
Crested auklets[16] *Aethia cristatella*	Crevice nesting	Visual checks 2 times a day VS every two days VS once a week of nests during incubation Chicks weighed every three days and at least one adult captured within 6 days of hatching VS chicks weighed every three days VS visual check of nests once a week Study carried out for two years (1996, 1997)	No Yes (in 1997, positive effect with higher disturbance resulting in higher fledging rate)	No Yes
Least auklets[16]	Crevice	Nest checks every day up to hatching then every	Yes (during	Yes

Aethia pusilla	nesting	2-4 days up to fledging with weights and measurements of chicks VS inspected 4 times after locating eggs, no weights plus disturbance while checking other species VS different location checked twice after locating eggs, no weights, minimal disturbance	incubation, no difference in fledging rates)	
Snowy egret[17] *Egretta thula*	Tree nesting	Captured and weighed chicks every second day after hatching, banded at 7-10 days for 8-10 days after banding VS chicks banded at 7-10 days. Both groups with regular nest checks.	No	No

(Rodway et al 1996)[1], (Conway & Garcia 2005)[2], (Hamer & Hill 1993)[3], (Cuthbert & Davis 2002) [4], (Blackmer et al 2004)[5], (Booth et al. 2000)[6], (Schultz & Klomp 2000)[7],
(Saffer et al 2000)[8], (Ballard et al 2001)[9], (Cairns 1980)[10], (Sandvik & Barrett 2001)[11], (Safina & Burger 1983)[12], (Verboven et al. 2001)[13], (Hockey & Hallinan 1981) [14], (Hull & Wilson 1996) [15](Fraser et al. 1999)[16], (Davis Jr & Parsons 1991)[17] ,(Angelier et al. 2010)[18], (Wheeler et al. 2008)[19] ,(Woehler et al 2003)[20]

Investigator disturbance within a wider context

As anthropogenic factors such as climate change, commercial fishing, habitat encroachment and impacts of feral species intensifies, biologists are increasingly required to monitor, understand and quantify the changes these agents bring about on wild animal populations (Minteer & Collins 2008). However, long-term monitoring of wild animal populations often involves procedures that could be perceived as invasive to individual animals, such as banding or tagging (McMahon et al. 2007). We would argue that the paucity of substantive research into these effects is a limiting factor in a balanced discussion of these issues (Wilson & McMahon 2006).

A major impediment to improving the general understanding of investigator disturbance is the tendency for scientists not to publish non-significant results (Koricheva 2003). Consequently, many non-effects of investigator disturbance are mentioned only in passing, or relegated to one or two sentences in a more general paper (*e.g.* Hamer & Hill 1993; Booth et al. 2000; Schultz & Klomp 2000; Cuthbert & Davis 2002). If these results remain unpublished then the *corpus* of knowledge does not develop and decisions and debates remain uninformed. Ideally, all research on wildlife should include a component to assess if the research is likely to have detrimental impacts. The inclusion of a well-designed, rigorous, and easily accessible component to research investigator effects in any new study would

contribute greatly to the body of knowledge available to stakeholders when developing proposals for wild animal research.

Acknowledgements

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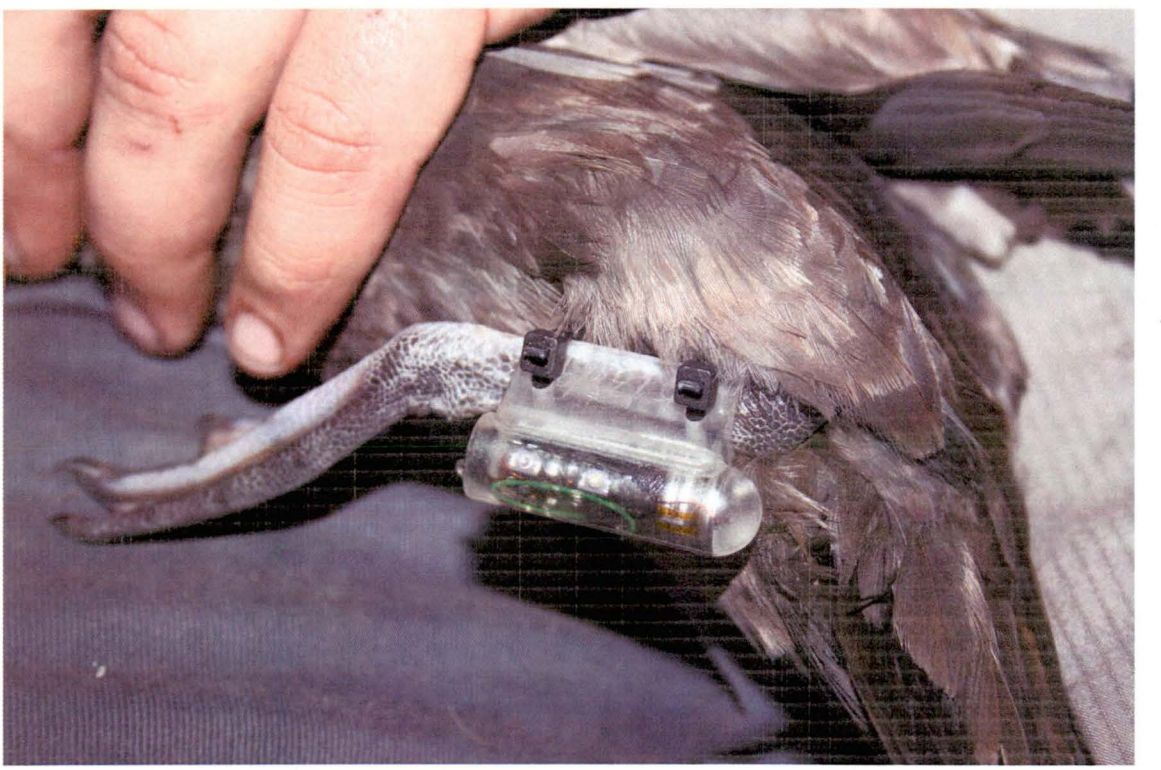
Chapter 4



Spatio-temporal use of the Southern Ocean by breeding short-tailed shearwaters (Puffinus tenuirostris)

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Keywords

Abstract

Short-tailed shearwaters are trans-hemispheric seabirds that breed in the Southern hemisphere during summer. During this time the birds rely on finding and exploiting productive zones in the Southern Ocean for successful breeding. Understanding where and how these birds use their Southern Ocean foraging grounds is therefore important for studying those factors determining population demography of this abundant Southern Ocean predator. We used archival data loggers to track 11 Short-tailed shearwaters breeding in southern Tasmania in the austral summers of 2005–2006 and 2007–2008 over the breeding season from pre-egg laying to late chick rearing. Trip characteristics changed between pre- and post-egg laying, with bimodal foraging strategies occurring once chicks had hatched and long trip duration contracting from 20.1 ± 10.6 days to 14.6 ± 2.2 days. Foraging occurred in a range of water masses from the Australian continental shelf to the Polar Frontal Zone with use of Southern latitudes increasing over the course of the breeding season. Overall we observed two types of long foraging trip pattern: 1) shorter trips that occurred closer to the colony, generally prior to breeding investment, mainly in coastal waters and incorporating area restricted search (ARS) behaviour, and 2) long 'looping' trips where birds left the colony, travelled south and foraged largely within the sub-Antarctic Zone and Polar Frontal Zone and returned to the colony on a direct heading.

Introduction

Seabirds are increasingly being used as monitors of environmental change (Furness & Camphuysen 1997) and large numbers of studies are attempting to link demographic parameters of seabird colonies to their biotic and abiotic environments (for a review see Tremblay et al. 2009). However, the ecological interpretation of the interactions between seabirds and their environment could be greatly improved with the use of *ad-hoc* statistical methods that facilitate pattern detection that can help to identify important foraging areas (such as area-restricted search) (Tremblay et al. 2009). In order to obtain this information and thereby improve the use of seabirds as indicators and make them more contextually relevant, further knowledge is required on their specific foraging locations and behaviours at sea (Durant et al. 2009).

Foraging locations for many marine predators have been successfully identified using a variety of tracking devices (Davis & Miller 1992; Bonadonna et al. 2000; Hindell et al. 2002), however, the costs associated with these technologies are often high with devices being bulky, heavy, or increasing drag and reducing foraging efficiency (Culik & Wilson 1991; Wilson & McMahon 2006; Burger & Shaffer 2008). Consequently there is paucity of data on the foraging locations of smaller petrel species, despite them being significant consumers of marine resources. Geo-location devices, while having reduced accuracy relative to GPS recorders and satellite transmitters, are lighter and have a reduced profile which makes them ideal to track smaller species. While these devices may only provide locations within an accuracy of 185-202 km (Phillips et al. 2004; Shaffer et al. 2005), for wide ranging pelagic species that may travel more than 1000 km per day such as many of the smaller petrel species (Klomp & Schultz 2000), this is an acceptable range of error.

Short-tailed shearwaters are a medium size petrel and are among the most prolific seabirds in the Southern hemisphere with an estimated population of 23 million birds (Bradley et al. 1991). Their biomass makes them significant consumers of

oceanic resources during the austral breeding season. However, despite their presence in Antarctic waters being reported as far back as 1940 (Routh 1949), little is still currently known of the specific geographic locations they utilise within the Southern Ocean.

A small population of short-tailed shearwaters at the southern most extent of their breeding distribution recorded an exponential rate of change of -15% per annum from an estimated 36 569 ± 7291 breeding pairs to 12 602 ± 1697 breeding pairs between 2003 and 2010, Chapter 1). As correlations between environmental variation and population demography have already been detected in other closely related petrel species that also use the Southern Ocean during breeding *(e.g.* sooty shearwater *Puffinus griseus* (Veit et al. 1996; Veit et al. 1997; Shaffer et al. 2006, 2009)), it follows that the observed decline of short-tailed shearwaters on Wedge Island may also be a consequence of changing oceanographic parameters affecting resource availability (quality and quantity). As the trend for Southern Ocean warming is expected to induce a latitudinal shift of fronts (Moore et al. 1999), it is possible that central place foragers such as breeding shearwaters will experience increased costs of foraging or changes in foraging distribution and habits which may affect their population demography (Inchausti et al. 2003; Bost et al. 2009). However, to determine whether this is indeed true requires detailed information on the at-sea movements of these birds.

Quantitative descriptions of use of the Southern Ocean by short-tailed shearwaters is currently limited to at-sea observations (Woehler et al. 2006), stable isotope analysis (Weimerskirch & Cherel 1998) and two satellite tracking studies (Klomp & Schultz 2000; Einoder & Goldsworthy, 2005). It is known that this species employs a bi-modal feeding strategy that consists of short trips (1–3 days) to provision chicks supported by dietary evidence of inshore species collected from adults at breeding sites (Serventy et al. 1971; Lindsey 1986), interspersed with long foraging trips of up to 17 days (mean 12 days) in which adult body condition is replenished in high latitude Antarctic waters (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994; Congdon et al. 2005). Bi-modal feeding strategies had previously been reported in several subantarctic procellariform species (Baduini &

Hyrenbach 2003) and are likely to aid in improving adult body condition and in reducing competition for inshore resources during the most energetically expensive phase of breeding (chick rearing) (Weimerskirch & Cherel 1998).

While it is known that the Southern Ocean is used by short-tailed shearwaters throughout the breeding season, the exact regions exploited by these birds are as yet unidentified. Therefore, the aims of this study were to identify the most important oceanographic regions for breeding short-tailed shearwaters throughout the various stages of the breeding cycle (pre-egg laying, incubation and chick rearing), to describe the spatial aspects of their foraging patterns and to identify and describe behavioural foraging modes such as Area Restricted Search (ARS behaviour).

Methods

Field methods

A total of 25 archival tags were deployed in December–January 2005 (n = 10 deployed, n = 6 retrieved), October–December 2007 (n = 10 deployed, n = 5 retrieved), and January–March 2008 (n = 5 deployed, n = 2 retrieved) on breeding short-tailed shearwaters at Wedge Island in Southern Tasmania (43° 08′ S, 147° 40′ E, n = 20 birds), (Table 4.1). The devices were a combination of Lotek LTD-2400 (mass = 5.5 g) and British Antarctic Survey (BAS) Mk3 geolocation tags (GLS) (mass = 9 g) tags. Lotek loggers were glued to a plastic cradle (2.5 g) and attached to the tarsus using small cable ties. BAS loggers were glued to a Velcro cuff and secured with Tesa tape to the tarsus. In both cases, the total mass of the unit and its attachment materials, represented 1.2–1.4% of the average adult body mass of shearwaters (650–700 g) on Wedge Is which is below the accepted threshold of 3–5% (Phillips et al. 2003) and comparable to tags deployed in other shearwater studies (Shaffer et al, 2006; Gonzalez-Solis et al. 2007; Carey et al. 2009.

All birds were captured in their burrows. When re-capturing a tagged individual, a one-way trap door was fitted at the entrance which prevented the birds leaving the burrow. These burrows were inspected hourly between dusk (18.30 h to 21.00 h depending on month) and midnight (*i.e.* when no more birds were seen to return to the island). Only one adult per pair had a logger attached, however, the sex of the tracked adults was unknown.

For the purposes of this paper, we refer to the oceanic frontal zones described by Orsi et al. (1995), Park et al. (1998) and Bost et al. (2009) and define the Southern zone (SZ) as temperatures between –1 °C to 2 °C, the polar frontal zone (PFZ) as temperatures from 2 °C to 5 °C, and the subantarctic zone (SAZ) as temperatures from 5 °C to 8 °C. The Australian shelf and coastal surface waters ranged from 8 °C to 23 °C.

Table 4. 1. Retrieved logger characteristics, including date collected, trip duration, distance (in km) and percentage of time spent in long trips.

logger ID	retrieved	trips > 3 days	trips < 3 days	total distance	% time at sea spent in long trips
A13944	12/07	3	0	12700	100
A13719	12/07	2	0	15200	100
A13718	12/07	3	0	14200	100
A13716	12/07	4	0	10400	100
BAS1	01/06	1	0	1500	100
BAS7	02/06	1	4	1700	84.62
BAS8	02/06	1	11	1100	56.00
A13719	03/08	3	6	15000	84.62
A13718	03/08	3	5	20000	90 57
A12986	03/06	2	6	13400	76.47

Statistical Methods

Data retrieval

Lotek LTD-2400 loggers were programmed to record light levels and temperature every 120 seconds for the duration of the deployment. BAS loggers recorded light levels every 60 seconds (subsequently summarised in 10 minute blocks) and did not record temperature data. Foraging trips were defined as the time that the bird left the burrow until it returned. Burrow occupancy was determined from the recorded light and temperature data with sharp increases in temperature (≥25 °C), in association with periods of low light levels (Thalmann et al. 2009) (Fig. 4.1).

Trip characteristics

Locations were estimated for each separate trip (both logger types) using the tripEstimation package (Sumner et al. 2009) in the R program (version 2.10.0, R

Development Core Team 2009). Unlike other light-level geo-location algorithms, this approach provides two locations per day, one for each twilight. Each point on the earth's surface has a distinctive twilight light curve which varies in shape predictably with longitude, latitude, and time of year. TripEstimation incorporates this information with the previous known locations of the animal, a range of possible flying speeds and sea-surface temperatures. The program returns each location with an associated probability distribution, which can be constrained to locations within the 95% confidence intervals of that distribution. The resulting tracks were separated into breeding stage (pre-egg laying, incubation, early chick rearing, and late chick rearing). Locations could only be derived from long trips as the short trips of less than 3 days did not provide enough information to be accurately assessed by the tripEstimation package.

NOAA Optimum interpolation (OI) sea surface temperature (SST)_V2 SST data (monthly; 1-degree resolution) were obtained from the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html) and

Ice coverage, Blended Optimum interpolation (OI) NCDC AMSR+AVHRR, 0.25 degree global monthly means were obtained from Bloomwatch (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp). Mean values of SST and ice-edge extent were isolated for the specific time periods relevant to the trips (*i.e.* pre-egg laying, incubation, early chick rearing, late chick rearing).

Trip duration between pre-investment (*i.e.* pre-egg laying) and post-investment (*i.e.* when the birds are constrained by the necessity to return to the breeding colony during incubation, early chick rearing and late chick rearing) was compared using a generalised linear mixed model (GLMM) in the lme4 package in R (Bates & Maechler 2009). Mixed models were preferred due to the lack of independence of data occurring as individuals were tracked through multiple time scales. Generalised linear mixed models are advantageous for the analysis of ecological data as they combine the properties of two statistical frameworks (linear mixed models that incorporate random effects) and generalised linear models (which handle non-normal data) (Bolker et al. 2009). Trip duration and breeding stage were designated fixed effects with bird included as a random effect.

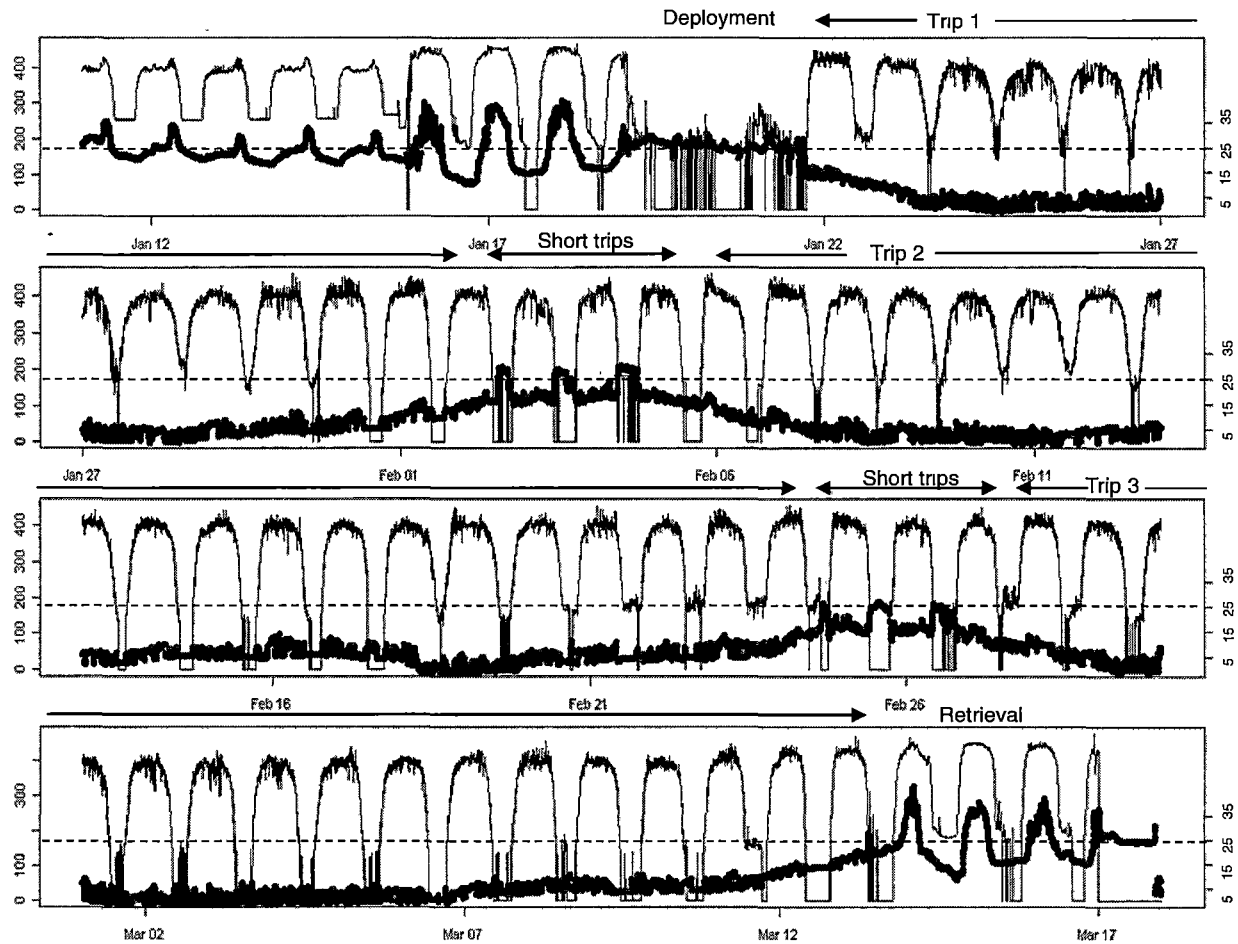

Fig. 4. 1. Puffinus tenuirostris: raw data from a bird equipped with a Lotek LTD-2400 data logger showing light and temperature (bold line, light scale on left hand y axis, temperature scale on right hand axis), time of deployment, long trips and short trips. Dashed line represents 25 °C and return to burrow.

A Poisson error distribution was used as examination of the residuals revealed this to be the most appropriate and restricted maximum likelihood (REML) used to estimate model fit.

Time spent in water masses

Owing to the low retrieval rate (<50% of loggers) our sample size was relatively small. Hence, to obtain a generalised view of behaviour at sea, temperature data was pooled from all individuals within the specific temporal frames. While fronts relate to the water column (*e.g.* the PFZ defined as the northernmost extent of the subsurface temperature minimum of 2 °C), this corresponds to SST of 4-5 °C in Summer (Park et al. 1998). Therefore, in the absence of diving temperatures, which would allow the construction of a temperature profile, we used SST to define the water masses. Water temperature was plotted as frequency distributions for each breeding stage for the long trips to demonstrate the proportion of time spent in differing oceanic regions (polar vs. coastal). A GLMM was used to compare the means of water temperature between breeding stages. Median SST and breeding phase were designated as fixed effects with bird included as a random effect and a Gaussian error distribution was used upon examination of the residuals and Laplace approximation used to estimate model fit. A 3 x 4 contingency table was used to assess time per trip spent in different water masses during the breeding season (PFZ, SAZ, Coastal x pre-egg laying, incubation, early chick rearing and late chick rearing).

Flying speed was calculated as distance between consecutive locations divided by time between those locations. Frequency distributions of the speeds for each breeding stage were plotted to demonstrate proportions of time with low speeds indicative of foraging or resting and higher speeds indicative of travel to prey patches or return to burrows. Mean speed between pre- and post-investment were compared using a GLMM. Speed was log transformed to normalise the data and speed and breeding stage were designated fixed effects with bird as a random effect. A Gaussian error distribution was used upon examination of the residuals

and Laplace approximation used to estimate model fit. Estimates of duration are presented as % ± standard deviation.

Identification of Area Restricted Search (ARS)

Location data can provide information on behavioural state and therefore to infer likely foraging areas. Predators are thought to increase their turning rate once they encounter prey or in response to environmental cues (Fauchald 1999). In a continuous patchy environment search effort is increased due to the likelihood of detecting other prey nearby (Kareiva & Odell 1987; Weimerskirch et al. 2007), a behaviour known as an area restricted search (ARS). State-space models (SSM) provide a platform with which to analyse the speed, distance, and turn angle derived from geo-location devices to provide a behavioural mode such as an ARS (Patterson et al. 2008). A state-space model couples a hypothetical mechanistic model (known as the process model) (Patterson et al. 2008) to an observation model based on the position of the animal. Therefore, the process model can predict the future state of the animal (variables such as spatial location or foraging mode) given its current state. The observation model weights the predictions based on the likelihood of the data and then links these back to the process model (Patterson et al. 2008). This has the effect of reducing confounding effects of behavioural inference from such variables as observational errors and changes in environmental conditions (Musyl et al. 2001; Patterson et al. 2008). State-space models were run using R and winBUGS to determine a behavioural mode representative of active foraging activity (ARS) and the resulting location of ARS overlayed on the tracks. A GLMM was used to compare time spent in ARS between pre- and post- egg laying (Poisson error distribution, days duration and time spent in ARS designated fixed effects with bird included as a random effect, REML to estimate model fit).

Results

Trip characteristics

Of the 25 loggers deployed in the two breeding seasons, 13 were retrieved from the birds and 11 held viable data among which we identified 23 long foraging trips (*i.e.* greater than four days duration) (Table 4.1). The trips occurred during four phases of the breeding cycle: pre-egg laying (n = 4 birds, n(tracks) = 9), incubation (n = 4, n(tracks) = 4), early chick rearing (n = 5, n(tracks) = 8), and late chick rearing (n=2, n(tracks) = 2). There were no trips of less than three days during either pre-egg laying or incubation; however, once chicks had hatched, trips switched to the bi-modal foraging strategy with parents alternating between a series of short (usually one day) trips and long trips. During the long trips, individual short tailed shearwaters exploited large oceanographic areas and were recorded at latitudes as far as 63.29 °S (at the ice-edge extent of the Antarctic continent) to 38.79 °S (in southern Victoria near the Australian mainland), and between longitudes of 100.16 °E to175.50 °E.

The mean length of long foraging trips across all stages was 16.7 ± 7.5 days. However, prior to eggs being laid when the birds were not constrained to the breeding site, long trips ranged from 5–46 days (mean 22 ± 3 days, Table 4.2). Once eggs were laid and incubation and chick rearing commenced, the variability in the duration of long trips contracted to a mean of 14 ± 2.6 days (GLMM, $Z = 3.61$, $df = 22$, $p<0.01$), Table 4.2).

Time spent in water masses

No short trips were observed during the pre-egg laying and incubation phases. Once eggs had hatched, birds feeding chicks (n = 5) spent 21.7 ± 14.6% during chick rearing in short-trips of one day duration. During short trips (< 24 hour duration), birds were foraging within Tasmanian coastal waters. This is likely to be within approximately 400 km from the breeding colony, which is half the maximum travelled distance by a bird in this study. Long trips occupied 386 of the 418 days recorded at sea. The proportion of time spent in different water masses over the

duration of the breeding season were not equal ($\chi^2 = 57.7$, df = 6, $p<0.01$) and varied between inshore coastal waters, the PFZ, the SAZ with some small observations recorded within the SZ (Table 4.2).

During pre- egg laying, foraging mostly occurred in inshore coastal waters with the remainder of observations distributed between the PFZ and SAZ ($\chi^2 = 6.81$, df = 2, $p<0.01$, Fig. 4.2a). Peaks in frequency occurred at 5 °C which denotes foraging on the northern edge of the PFZ (close to the SAZ), and 15 °C indicating foraging closer to the coast of Tasmania. Mean speed per trip during this time was significantly lower than for the rest of the breeding season (GLMM, t = 2.9, df = 553, $p<0.01$) as the birds were not yet constrained by the necessity of returning to the breeding site to either swap incubation shifts or to feed chicks.

During incubation and chick rearing, (n = 4, n(tracks) = 4, n = 5, n(tracks) = 10 respectively), trips were significantly shorter in duration than during pre-egg laying (GLMM, Z = 2.32, df = 22, $p<0.01$) although the total distance travelled during these trips was analogous ((GLMM, t = –1.2, df = 22, p = 0.2), Table 4.2) signifying that the birds were travelling similar distances in a shorter time period. Foraging during incubation occurred mostly north of the PFZ ($\chi^2 = 20.2$, df = 2, $p<0.01$) with temperature frequencies peaking at 5 °C to 7 °C and 12 °C to 17 °C (Fig. 4.3b) however during early and late chick rearing (n = 5, n(tracks) = 10), foraging shifted further south ($\chi^2 = 6.82$, df = 2, $p<0.03$, $\chi^2 = 8.76$, df = 2, p = 0.01), with the majority of foraging occurring in the PFZ and SAZ (Fig. 4.3c, d) and some foraging occurring at the extent of the ice edge in that year (Fig. 4.2 b, c, d).

Area Restricted Searches

Area Restricted Search behaviour was identified in 11 of the 23 tracks (Table 4.2). Within trips with ARS behaviour the percentage of time spent engaged in this behavioural mode ranged from 3–100% of the total trip duration. However, those trips that exhibited 100% of time spent in ARS were only recorded using the BAS Mk3 loggers that have fewer records than the Lotek. Subsequently, the ssm results from these loggers are interpreted with some caution. Trips displaying ARS were significantly slower (GLMM, t = 10.0, df = 12, $p<0.01$) with mean speeds =

7.3 ± 2.8 km^{-1} as compared to mean speeds = 14.1 ± 3.8 km^{-1} than for those trips with no ARS. They also covered less distance (GLMM, t = 4.27, df = 12, $p<0.01$), mean = 3014 ± 2540 km than those that recorded no ARS mean = 5800 ±

Table 4. 2. Trip variables from tracked birds. Speed is in km hr^{-1}, distance in km, time spent in ARS and water masses expressed as a percentage of the total trip duration.

Long trip ID	duration (days)	breeding stage	mean speed	mean dist	max speed	max dist	total dist	% time in ARS	% time in Coastal	% time in SZ	% time in PFZ	% time in SAZ
A13944 1	16	pre-laying	7.7	93.4	23.9	286.5	3081.7	77.6	37.5	0.0	25.0	37.5
A13944.2	21	pre-laying	11.3	145	40.7	541.1	6236.8	0	100 0	0.0	0 0	0.0
A13719.1	19	pre-laying	4.2	50.9	12.8	154.1	1884.5	66.7	100.0	0.0	0.0	0.0
A13719.2	25	pre-laying	12.5	165.2	41.4	613	8427.5	0	8.0	8.0	60.0	24.0
A13718 1	46	pre-laying	9.12	109.49	53.5	641 9	10183.3	64 2	47 0	0.0	10.0	43.0
A13716.1	19	pre-laying	5 4	66	15 7	246	2604.2	66.2	73.0	0.0	0.0	27.0
A13716 2	12	pre-laying	6 2	73.9	19.1	229.3	1848 5	100	100.0	0.0	0.0	0 0
A13716.3	5	pre-laying	12.1	143.4	34.5	414.4	1577.8	82.6	79.0	0.0	0.0	21.0
A13716.4	18	pre-laying	9.3	117.1	48 2	578 4	4334 2	70.7	0.0	0.0	56.0	44.0
BAS1.1	14	incubation	3.9	55.8	11 4	138.7	1506.9	100	n/a	n/a	n/a	n/a
A13944.3	16	incubation	8.2	109.8	25.8	378.5	3404	0	100.0	0.0	0.0	0 0
A13719 3	13	incubation	13 6	179 8	52.8	681.8	4853 5	0	7.7	0.0	23.0	69.3
A13718 2	15	incubation	9·6	130 4	33.5	552	4043.5	0	73.0	0.0	0.0	27 0
BAS7 1	18	early chick	11 2	45.4	7	97.5	1680	100	n/a	n/a	n/a	n/a
BAS8.1	11	early chick	3.9	46.8	9.6	516 7	1443.8	7.9	n/a	n/a	n/a	n/a
A13719March.1	11	early chick	11.5	156.2	28.3	411.2	3593 6	0	18.0	0.0	82.0	0.0
A13719March.2	18	early chick	13.9	181 5	44.6	535.4	6718	0	6.0	0.0	56 0	38 0
A13718March.1	14	early chick	16 8	221 8	58 2	823.6	5987.6	0	8.0	0 0	38 0	54 0
A13718March.2	19	early chick	16	207.6	50.8	663.6	7891	0	22.0	0.0	39.0	39.0
A12986.1	11	early chick	22.2	288	58.4	700.9	6067.5	0	30.0	0 0	30.0	40.0
A12986.2	15	early chick	20.2	254	44.9	651	7384	0	43.0	7.0	21.0	29.0
A13719March.3	15	late chick	12.1	149 7	15 6	372 2	4643.2	0	13.0	8.0	44.0	25.0
A13718March.3	15	late chick	15 7	198.4	32.7	413.6	6150.6	0	7.0	0.0	53.0	40.0

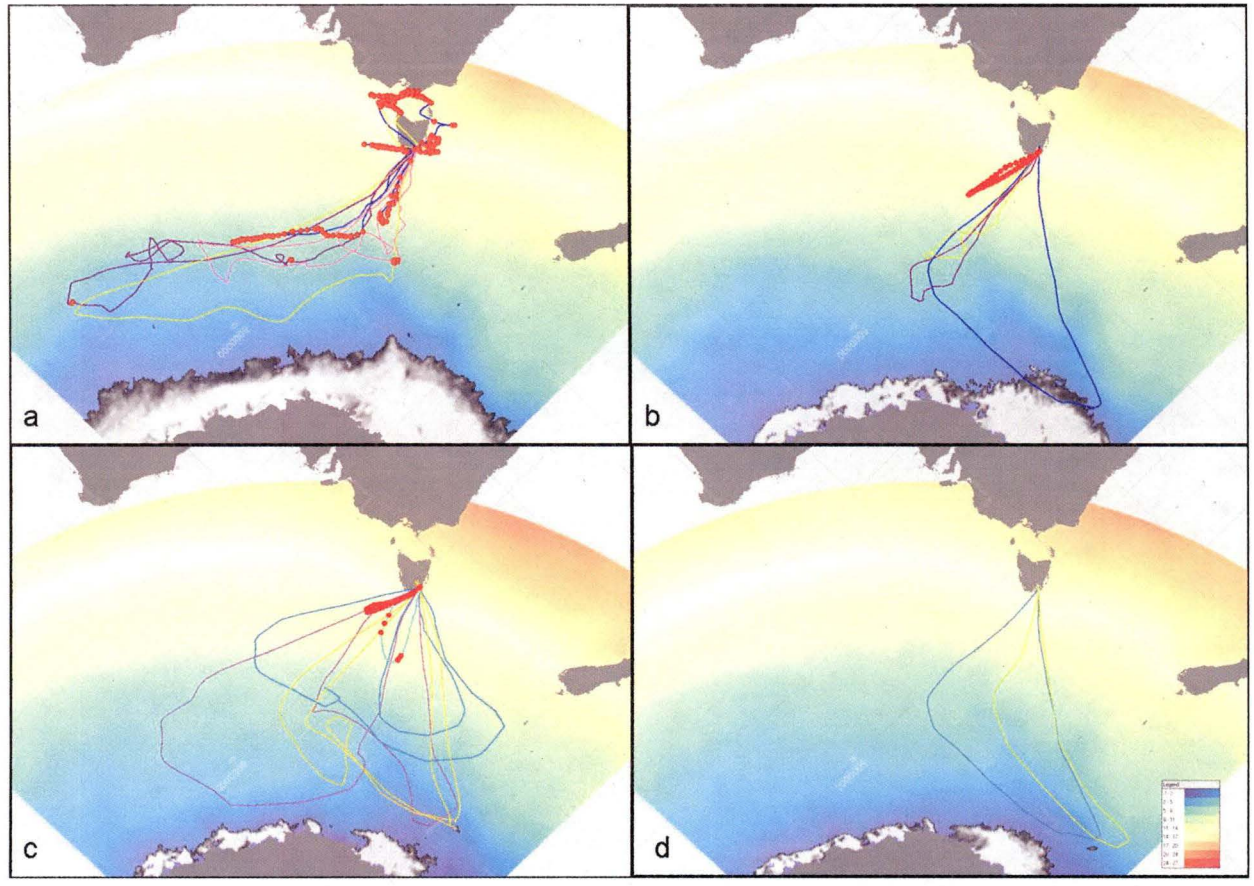

Fig. 4. 2. *Puffinus tenuirostris*: tracks from geo-logged short-tailed shearwaters during the breeding seasons of 2005–06 and 2007–08; a) pre-egg laying; b) incubation; c) early chick rearing; and d) late chick rearing. Mean monthly sea ice extent for each breeding period is shown surrounding the continent edge and mean monthly sea-surface temperature for the breeding phases. Red points are area-restricted search (ARS).

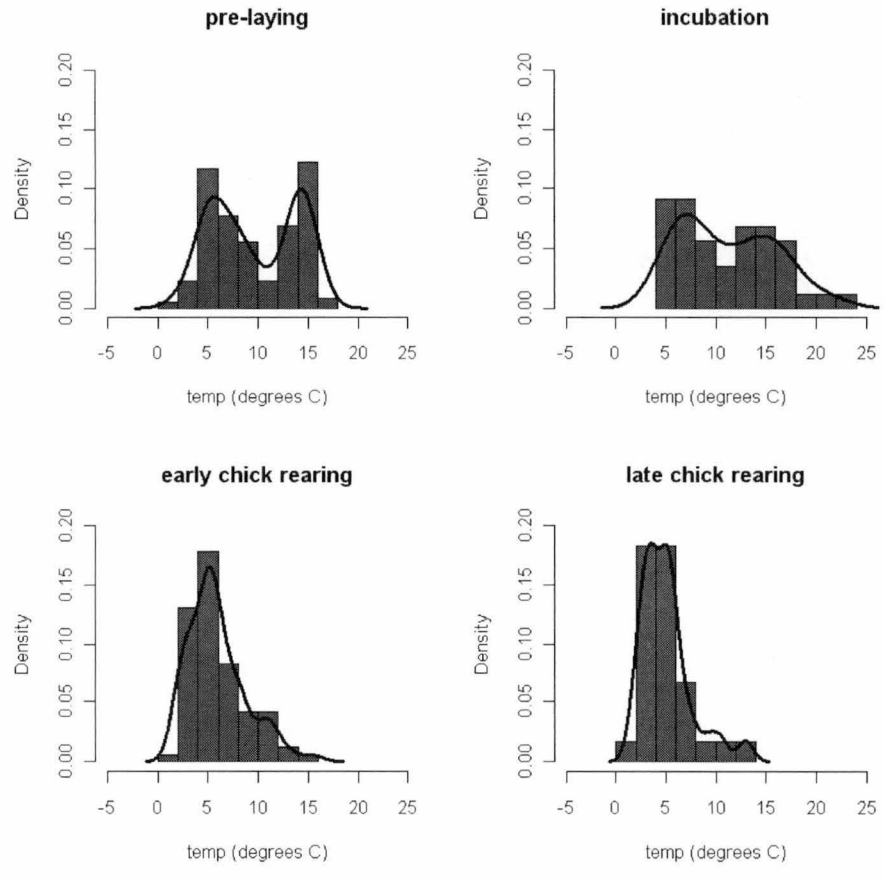

Fig. 4. 3. Puffinus tenuirostris: frequency distribution of a) pre-egg laying nightly median water temperature during long trips; b) incubation nightly median water temperature; c) early chick rearing nightly median water temperature; and d) late chick rearing nightly median water temperature. All are plotted with density curves.

1543. Most of the ARS behaviour occurred in the early part of the breeding season during the pre-egg laying trips with one example during incubation and two during early chick rearing, however it should be noted that these latter modes were obtained from BAS loggers for which no temperature data was recorded and hence the relative time spent in water masses during ARS is unavailable for these tracks. During pre-egg laying, ARS was disproportionate across water masses (χ^2 = 22.02, df = 2, $p<0.01$) with the majority of ARS occurring in Australian shelf and coastal waters (62.4 ± 33% of total time) with some recorded in the PFZ (13 ± 9% of total time) and SAZ (24 ± 17% of total time) (Fig. 4.2a, b, c).

Long foraging trips therefore displayed two distinct patterns: 1) those with slower mean travel speeds that occurred closer to the colony, generally prior to breeding, mainly in coastal waters and incorporating the ARS behavioural mode, and 2) long looping trips where birds left the colony, travelled directly to feeding grounds, largely within the SAZ and PFZ and then returned to the colony on a direct heading. These trips were characterised by faster travel speeds, greater distances and occurred generally once eggs had been laid. Subsequently we have identified two spatial boundaries (inshore: 38–45° S and 142–152° E) and offshore (62–45° S, and 100–175° E) in which foraging is occurring providing a spatial reference that can be measured against environmental variability.

Discussion

In order to understand the mechanisms driving the population demography of seabirds, their interactions with the marine environment need to be integrated with their spatial use of geographic foraging locations (Durant et al. 2009; González-Solis & Shaffer 2009). This is the first study of its kind to successfully describe the spatial use of the Southern Ocean by individual short-tailed shearwaters throughout the entirety of their breeding cycle (including the pre-investment 'honeymoon' trip). Short-tailed shearwaters from Wedge Island utilised three distinct water masses, the PFZ, the SAZ and Australian shelf and coastal waters with three types of foraging trips that varied in length, behavioural pattern and rate of travel according to breeding stage.

Energetic demands of seabirds vary according to the time of the year and phase of life-cycle (Erikstad et al. 1998). The most conspicuous pattern observed in this study was the difference in foraging characteristics between pre- and post-investment. Although sample sizes are small, and further study on the spatial movements of these birds is necessary, the observed differences in trip characteristics were pronounced with pre- egg laying trips exhibiting slower travel speeds, higher latitudes and more ARS behaviour than trips made after eggs were laid. Short-tailed shearwaters undertake an annual migration to the Bering Sea during the austral winter and return to the breeding colonies in the middle of the austral spring. Upon return to the breeding colony, body condition is generally poor as adults have had to traverse the relatively unproductive central Pacific Ocean (Nicholls et al. 1998). However, this is also the most likely period of gametogenesis (Marshall & Serventy 1956) and a self-provisioning trip upon return to the breeding site (where mating occurs after the migration) is needed to restore the body condition lost during the trans-hemispheric migration. Subsequently, the pre-egg laying stage represents a critical time period influencing the likelihood that a bird will breed. Late September is generally the time of maximum sea ice extent and while it is not the most productive time in the Southern Ocean, it does signify the onset and an increase in biological productivity related to up-welling events, the destratification of water masses, and ice-melt blooms (Constable et al. 2003).

Short-tailed shearwaters feed on a diverse range of prey and exploit different prey for chick feeding and self provisioning (Weimerskirch & Cherel, 1998). Trip characteristics identified in this study were consistent with exploiting a range of prey. Previously, dominant items found in stomach samples have comprised *Nyctiphanes australis,* a euphausiid which is found in Australian coastal and shelf waters from 31–44° S and 132–156° E (Blackburn 1980), and studies have found a high proportion of *Nyctiphanes* in the diet in September/October (Skira 1986) which corresponds to the breeding season and swarming of this animal. When feeding offshore however, the most important prey items identified in diets from both stomach samples and stable isotope studies comprise *Euphausia superba* (Kerry et al. 1983), *Euphausia vallentini* (Weimerskirch & Cherel, 1998), various squid species and mycotophid and post larval fish (Skira, 1986; Weimerskirch & Cherel, 1998). These organisms are found in waters ranging from the sub-Antarctic front to the most Southern waters nearing the ice-edge extent of the Antarctic continent (Pauly et al. 1998; Weimerskirch & Cherel 1998), but vary in their distribution, abundance, and behaviour (also see chapter 5).

As prey distribution and abundance varies both spatially and temporally, predators employ a range of behavioural modes to counteract the unevenness of prey distribution in the ocean and increase their rate of encounter (Kareiva & Odell 1987). It is surprising therefore, that in such a dynamic environment where prey is often patchily distributed, studies that are analysing behavioural modes in pelagic seabirds are not reporting ARS as the dominant behavioural foraging mode. Wandering albatross spend only 23% of their time in ARS modes (Weimerskirch et al. 2007) and while ARS behaviour was detected at rates of 59% ± 11% during pre- investment foraging in our study, this was temporally specific with rates of ARS occurring only at 14% ± 9% once investment had occurred. The lack of ARS once birds were constrained to the breeding site by the need to switch incubation shifts or provision their chicks, may be explained by spatial scale at which pelagic seabirds operate. Zollner & Lima (1999) predicted that straight-line search is effective across a range of conditions and that subsequently the paths of animals searching across long distance should be typically (but not absolutely) straight.

They also predicted that dispersing animals with limited energy reserves should move in straighter paths than those with greater energy reserves. Thus as postulated by Weimerskirch et al. (2007), the second type of foraging pattern (looping trips) where birds appear to be moving directly to foraging grounds on what has previously thought to be a commuting phase may in actual fact be the main searching strategy for large-scale foragers.

Looping trips have been reported for a number of pelagic seabirds (Sagar & Weimerskirch 1996; Hull et al. 1997; Weimerskirch et al. 2005, 2007). For short-tailed shearwaters in our study, this pattern was observed more frequently once eggs had been laid and birds were constrained to by necessity to return to the breeding site. The post investment period also coincided with the start of the bi-modal feeding strategy where adult birds were alternating between short and long trips. Bi-modal feeding strategies in part serve to reduce competition for inshore resources (Weimerskirch & Cherel 1998) but may also provide a buffer against poor foraging conditions by allowing greater flexibility in foraging habitat choice (Shaffer et al. 2009).

The early and late chick rearing periods showed the most southerly ranging trips with the majority of foraging occurring within the PFZ and SAZ and some tracks extending to the sea ice in that year. This supports observations made by Woehler et. al. (2006) that birds exploit the edge of the sea-ice around the Antarctic continent which corresponds to the highest concentrations of Antarctic krill and the areas of highest primary productivity (Pauly et al. 2000; Constable et al. 2003). While previous diet studies have reported high percentages of myctophid fish in the diet during long trips (Cherel et al. 2005), this study would suggest that adult birds in this season were exploiting more southerly resources and may infer that inter-annual variability in foraging patterns may be occurring (see chapter 5).

Trip characteristics of this time period may also be influenced by foraging site fidelity. The temporal variation of marine environments mean that surrogate measures of variation such as reproductive output or body condition may provide

an alternative to the immediate assessment of habitat quality (Schmidt 2001). Long-lived species such as seabirds may develop an energetic advantage by remaining faithful to regions of potentially high productivity (Bradshaw et al. 2004) and the consistent use of the PFZ and SAZ during the most energetically expensive period of the breeding season (Woehler et al. 2006) may be a reflection of prior knowledge of the energetic value of this region of the Southern Ocean. However the consequences of foraging site fidelity in the context of protracted environmental variability may result in overall effects on population demography of Southern Ocean predators, although the direction of effects is still to be determined for many species.

Profound responses to increasing environmental variability within the Southern Ocean have already been recorded in a number of species (Parmesan 2006), including sooty shearwaters, a species that overlaps with the foraging range of short-tailed shearwaters during the breeding season (Shaffer et al. 2009). Antarctic circumpolar fronts (ACC) have already begun to move up to 60 km south (Sokolov & Rintoul 2009b) and it has been predicted that this southward shift of ocean fronts may increase the cost of foraging for some predators exploiting the Southern Ocean (Inchausti et al. 2003; Bost et al. 2009), although the mechanisms associated with this are uncertain. Identifying the most important foraging locations may assist in understanding how changing environmental conditions are likely to affect the species that use these areas. While obtaining, interpreting and relating spatial information to ecosystem interactions is not always simple, the increasing body of knowledge will be crucial for understanding the mechanisms behind predator responses to environmental variability.

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Chapter 5

Chapter 5

Variability in the adult provisioning diet and reproductive performance of a pan oceanic predator; the short-tailed shearwater (*Puffinus tenuirostris*)

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Abstract

Increasing oceanographic variation within the Southern Ocean is expected to influence predators, but the nature of the influence is unknown. Obtaining information on foraging locations and diet of marine predators will assist in determining the mechanisms driving the influence of environmental variation on upper trophic consumers. The diet of a major Southern Ocean predator, the short-tailed shearwater, was measured over four years using stable isotopes. Stable isotope analysis of whole blood indicated inter-annual differences in diet during the four years of the study with $\delta^{13}C$ and $\delta^{15}N$ values in 2004–05 and 2005–06 significantly higher than in 2006–07 and 2007–08. An isotopic mixing model suggested that the 2004–05 and 2005–06 breeding seasons were dominated by higher trophic prey such as fish post-larvae and sub-Antarctic Euphausiids that were assimilated in water masses from the coast of Tasmania to the Polar Frontal Zone (PFZ). In contrast, the 2006–07 and 2007–08 seasons were dominated by lower trophic prey, suggested by a multi-mixing model as Antarctic and sub-Antarctic euphausiids and Antarctic squid sourced from water masses south of the PFZ. Despite the contrast in diet between seasons, we detected no direct relationship between prey type and reproductive performance for the four years of the study, indicating that short-tailed shearwaters are flexible in their response to changes in prey availability.

Introduction

The mechanisms driving the effect of climate on trophic interactions are still poorly understood (Cherel & Hobson 2007; Beaulieu et al. 2009). To quantify and understand these drivers often requires long-term data sets, with seabird species offering data on linkages between physical processes and population performance (Sandvik et al. 2005; Cherel et al. 2007). Climate influences animal populations through a number of processes including: their foraging behaviour, diet, reproductive success, growth rates, migration patterns and timing of seasonal activities. These influences may be intrinsic (relating to metabolic processes, reproduction and density dependence) or extrinsic (relating to availability of prey and competition) (Durant et al. 2007).

Measuring the diet of seabirds is one of the simplest ways to detect environmental variation as it provides information on availability and abundance of the lower trophic organisms that form the base of food webs. However, classic diet measurement approaches such as stomach contents analysis is often only available for a small fraction of the annual cycle of a population, typically when they are feeding chicks (Quillfeldt et al. 2005). Procellariiformes seabirds frequently employ a bimodal feeding strategy during the breeding season that sees them alternate short feeding trips of one or two days in close proximity to the breeding colony, and long trips of up to 17 days that exploit more distant resources (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994; Congdon et al. 2005). Diet during long trips cannot be measured using diet samples as the stomach contents are mostly digested before the animal returns to the breeding location and biased towards hard parts such as beaks and otoliths (Quillfeldt et al. 2005). Consequently, alternative methods that incorporate a longer temporal window are important in understanding the resources that are being exploited during long trips.

Stable isotopes are increasingly being used to infer long-term diet and spatial patterns of foraging (Inger & Bearhop, 2008) and to date numerous studies have applied stable isotope analysis in determining the diet and foraging locations of

seabirds (for a review see Forero & Hobson 2003 and Phillips et al. 2009). Isotopes are useful tools to measure diet as lighter isotopes are preferentially excreted and the remaining tissues become enriched with the heavier isotope (Owens 1987). In marine consumers Nitrogen 15 ($\delta^{15}N$) generally increases by 2–5% per trophic level and can be used to infer trophic position (Owens 1987; Hobson & Welch 1992) whereas Carbon 13 ($\delta^{13}C$) increases at 0.8–2% and reflects the Carbon levels at the base of the food chain (DeNiro & Epstein 1978; Kelly 2000; Cherel & Hobson 2007) and can therefore be used to estimate food source location as phytoplankton inshore typically have higher levels of Carbon than those offshore (Kelly 2000). Carbon is also strongly associated with individual water masses, for example, values are relatively constant within the Antarctic zone and increase strongly at the sub Antarctic and polar fronts (Trull & Armand 2001). Other advantages of stable isotope analysis include the ease of obtaining large samples and the minimally invasive techniques required to do so (Hodum & Hobson 2000).

As reproductive performance (*i.e.* the number of offspring produced per breeding pair) varies significantly both inter-annually and during longer time scales (Aebischer & Coulson 1990; Montevecchi 1993; Sydeman et al. 2001), diet studies represent the intermediate link between environmental variability and population demography. Reproductive performance of many seabirds is easily measured and provides real time information on the relationship between performance and prey availability (Sydeman et al. 2001). Therefore, while measuring diet from inference methods like stable isotopes is useful in terms of understanding the exploitation of specific resources, in order to ascertain what kind of effect those resources are having, the measurement of reproductive success in tandem with inference methods provides the direct impact of resource availability (Pat Herron Baird 1990; McMahon et al. 2009).

Short-tailed shearwaters (*Puffinus tenuirostris*) are medium to large petrels with a trans-hemispheric distribution that breed around south-eastern Australia during the austral summer and migrate to the Bering sea during the austral winter (Marchant et al. 1990). They are also one of the most numerous seabird species with the

current population estimated at 23 million individuals (Bradley et al. 1991). Their high biomass makes them significant consumers of marine resources (Brooke 2004) and tracking has demonstrated that they utilise a vast area of the southern ocean, ranging from coastal waters surrounding their breeding colonies to the ice-edge extent of the Antarctic continent (Chapter 4). However, tracking information is still scarce and therefore the relative importance of water masses exploited during the breeding season can be provided using stable isotopes as a proxy of latitudinal distribution.

Previous studies have reported that short-tailed shearwaters employ a bimodal feeding strategy during the breeding season (Weimerskirch & Cherel 1998; Klomp & Schultz 2000), alternating between short feeding trips to provision chicks and long feeding trips to re-establish adult body condition. Diet during long trips, inferred by a simple isotopic mixing model, has previously been reported from a single year to contain 87% myctophid fish and 13% sub-Antarctic krill (Cherel et al. 2005) based on isotopic blood plasma. Other contributing species have included the hyperiid amphipod *Themisto gaudichaudii*, the Euphausiids *Euphausia vallentini*, *Euphausia superba* and *Nematoscelis megalops* and post-larval fish. Short-trip diet, when adults are provisioning chicks, comprises prey belonging to different ecosystems. These range from the pelagic oceanic Antarctic ecosystem in the South to the pelagic, neritic Tasmanian ecosystem near the breeding colony in the north (Cherel et al. 2005). In addition to food consumed by adults, short-trip diet contains higher rates of prey items such as *Nyctiphanes australis* and the cephalopod *Notodarus sloani gouldi,* which are found in Australian shelf and coastal waters (Cherel et al. 2005). Previous studies of the wintering diet of the short-tailed shearwater have demonstrated that they show plasticity in their foraging in response to inter-annual variability in prey availability, changing their diet from crustaceans to fish in years when crustaceans were less available in their foraging grounds (Hunt et al. 2002).

Here we compare four years of isotopic data taken three times at monthly intervals during the breeding season and examine the prey exploited when adults return from long trips of up to 19 days (Chapter 4). This will allow us to 1) identify

seasonal and annual differences in the diets of short-tailed shearwaters and determine the effect of changes in diet (if any exist) on survival and fledging mass of chicks, 2) compare the $\delta^{13}C$ values of short-tailed shearwaters to tracks obtained from geo-location in order to clarify latitudinal foraging zones and 3) compare the isotopic signatures of short-tailed shearwaters to other Southern Ocean predators.

Methods

Chick survival and fledging mass

Field work was conducted on Wedge Island (43° 07' S, 147° 40' E) in Southern Tasmania, Australia. The population of short-tailed shearwaters was estimated as 36 569 ± 7291 in 2003 but has declined to 12 602 ± 1697 in 2010. Reproductive success was estimated using a stratified sampling regime. Circular quadrats (n = 241), to reduce edge effects were distributed over the entire island encompassing 641 burrows which were monitored from 2003–2010. The annual rate of egg laying was calculated as mean eggs per quadrat ± standard error (SE). Reproductive success was calculated as chicks fledged from eggs laid within quadrats ± SE. Mean fledging mass was calculated from a subset of 50 shearwater chicks, weighed and measured each month from hatching until fledging.

Foraging locations using geo-location

Lotek LTD-2400 (Lotek wireless) geo-location devices were placed on two birds in the 2007–08 season. For detailed attachment methods, see Chapter 4.

Sampling methods

Blood samples were collected from adult short-tailed shearwaters in the austral summers of 2005, 2006, 2007 and 2008 (n = 46, 65, 66 and 66 respectively) at three points during the breeding season, January (early chick rearing), February (mid chick rearing) and March (late chick rearing). Adult shearwaters were captured by hand upon their evening return to breeding burrows and 1.5 mL of blood was taken from the web vein of the foot using a 26 gauge needle and syringe. Samples were kept on ice *in situ* and then frozen immediately upon return from the island.

Samples of whole blood were dried at 60 °C for 36 hours and analysed using a Micromass Isochrom (Manchester, UK) continuous-flow isotope-ratio mass spectrometer. Stable isotope abundances were expressed in δ-notation as the

deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is 13C or 15N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Values were relative to Pee Dee Belemnite (PDB) and atmospheric N_2 (Air) for C^{13} and N^{15}, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors 0.15‰ and < 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope analysis was conducted at the Stable Isotopes Lab, by Environmental Biology Group, Research School of Biological Sciences Australian National University (ANU).

As the turnover of cells in whole blood is representative of a 2–4 week turnover in isotopes, (Bearhop et al. 2002), bloods sampled on January 20 ± 5 days were representative of the diet during incubation, bloods sampled on February 20 ± 5 days represent early chick rearing, and bloods sampled on March 20 ± 5 days represent mid to late chick rearing.

Statistical Methods

Chick survival and fledging mass

A linear model (Gaussian distribution, log link) was used to identify trends in survival and fledging mass and to test if survival and fledging mass were significantly different between years (n = 4). Survival and fledging mass were plotted against mean $\delta^{15}N$ and $\delta^{13}C$ for the four year data set.

Foraging locations using geo-location

Upon retrieval of the geolocation device, locations were estimated for each separate trip using the tripEstimation package (Sumner et al. 2009) in the R program (version 2.10.0, R Development Core Team 2009). Unlike other light-level geo-location algorithms, this approach provides two locations per day, one for each twilight. Each point on the earth's surface has a distinctive twilight light curve

which varies in shape predictably with longitude, latitude, and time of year. TripEstimation incorporates this information with the previous known locations of the animal, a range of possible flying speeds and sea-surface temperatures. The program returns each location with an associated probability distribution, which can be constrained to locations within the 95% confidence intervals of that distribution.

Definition of water masses was taken from Orsi et al. (1995), Park et al. (1998) and Bost et al. (2009) and define the Southern zone (SZ) as having sea surface temperatures between –1 °C to 2 °C, the polar frontal zone (PFZ) as temperatures from 2 °C to 5 °C, and the subantarctic zone (SAZ) as temperatures from 5 °C to 8 °C. The Australian shelf and coastal surface waters ranged from 8 °C to 23 °C. A chi square test was used to assess relative time spent in water masses for these two trips, based on the median nightly SST in association with the definition of water masses.

Isotope analysis

We used cluster analysis to identify groupings within the isotopic signatures of the four year data set by means of generating a similarity matrix using usual square distance between the two vectors (Euclidean distance) to detect annual and seasonal effects.

Isotopic signatures from whole blood of other Antarctic seabird predators, king penguin (*Aptenodytes patagonicus*), Adelie penguin (*Pygoscelis adeliae*), emperor penguin (*Aptenodytes forsteri*), Antarctic petrel (*Thalassoica Antarctica*) and plasma isotopic signatures from short-tailed shearwater chicks were sourced from Hodum & Hobson 2000; Cherel, Hobson, & Weimerskirch 2005; Cherel et al. 2007 and Cherel 2008 in order to determine trophic and latitudinal overlap with the shearwaters from this study.

Stable isotope analysis can be used to determine the contribution of food sources to the diet of predators (Hobson 1999; Phillips 2001) as the similarity of animal

tissue ratios with food source ratios gives a theoretical framework of their relative importance in the diet (Phillips 2001). Whilst previous approaches have used geometric procedures to quantify the contributions of up to three food sources for two elements (*e.g.* C and N, see Ben-David et al. 1997; Ben-David et al. 1997), concerns have been raised as to the accuracy of the output (Inger & Bearhop 2008; Moore & Semmens 2008). The recent introduction of Bayesian statistics for developing mixing models for application with stable isotope analyses has greatly reduced previous errors associated with estimating the proportion of prey in the diets of predators. This is because these approaches allow the incorporation of uncertainty in source isotopic values and fractionation factors (Parnell et al. 2010).

Likely diets were calculated using the *siar* package (Stable Isotopes in R, Parnell et al. 2008). This takes data on predator isotopes and fits a Bayesian model to potential based upon a Gaussian likelihood with a mixture dirichlet-distributed prior on the mean (Parnell et al. 2008). The isotopic values of delipidated prey were sourced from a number of studies (Table 5.1), although we recognise that for *E. vallentini, Nyctiphanes australis, Themisto gaudichaudii, Nematoscelis megalops* Cherel et.al. (2005) as prey was partially digested, carbon and nitrogen values may have been underestimated (Cherel 2008). The selected myctophid species were identified by fatty acid analysis as most dominant in the long trip diet of short-tailed shearwaters (Connan et al. 2005). Discrimination factors for nitrogen (2.7 ± 0.4) were taken from (Cherel et al. 2005) as the recommended mean for wild fish eating species. No correction was used for Carbon although we recognise that care must be taken in the choice of discrimination factors to apply to species for which no experiments on captive individuals have been or can be done as is the case with short-tailed shearwaters (Cherel et al. 2005). The model was used to infer diet for the two groups identified by the cluster analysis.

Table 5. 1. δ15N and δ13C signatures (means ± SD) for delipidated possible prey items of short-tailed shearwaters.

Prey	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Source
Nyctiphanes australis	11.7 ± 0.3	-20.4 ± 0.3	(Cherel et al. 2005)
Euphausia vallentini	-0.7 ± 1	-23.4 ± 0.3	(Cherel et al 2005)
Euphausia superba	3.01 ± 0.8	-24.8 ± 0.9	(Tierney et al. 2008)
Nematoscelis megalops	9.5 ± 1.2	-21.7 ± 0 6	(Cherel et al 2005)
Themisto gaudichaudii	1.6 ± 1 8	-23 2 ± 0 6	(Cherel et al. 2005)
Electrona antarctia	8.9 ± 0 3	-21 ± 0.5	(Cherel et al. 2010)
Kreffichythes anderssonii	7.6 ± 0.2	-22 3 ± 0 2	(Cherel et al. 2010)
Gymnoscopelis braueri	9.8 ± 0.3	-22.3 ± 0.7	(Cherel et al. 2010)
Fish post-larvae	5 6 ± 0.8	-20.5 ± 0.7	(Cherel et al 2005)
Pleuragramma antarcticum	10.6 ± 0.3	-24.7 ± 0.4	(Cherel et al. 2008)
Histioteuthidae	10 4 ± 0.7	-20.7 ± 0.4	(Cherel et al 2008)
Gonatidae	13.3 ± 0.5	-21 ± 0.8	(Cherel et al 2008)
Notodarus gouldi	12.8 ± 0.9	-19 ± 0.4	(Chiaradia et al, in press.)
Psychroteuthis glacialis	6.6 ± 1.06	-24 7 ± 0.7	(Zimmer, Piatkowski, & Brey 2007)

Results

Chick survival and fledging mass

Survival and fledging mass displayed no overall trend ($F_{1, 497} = 1.329$, $p = 0.25$, $R^2 = 0.00$) for the four year data set, although survival was significantly different between years ($F_{4, 341} = 206.8$, $p<0.01$, $R^2 = 0.7$) as was fledging mass ($F_{4, 56} = 571.3$, $p<0.01$, $R^2 = 0.97$) demonstrating that there were years of good and poor reproductive performance. Survival of chicks was lower in 2005 and 2008 than in 2006 and 2007 and fledging mass was low in 2008 and analogous in the other years (Fig. 5.1).

Foraging locations using geo-location

Foraging for the two birds with trackers demonstrated little activity within Australian shelf and coastal waters during this time period, with foraging occurring mostly within the PFZ and SAZ ($\chi^2 = 25.91$, df = 2, $p<0.01$) and some at the extent of the ice edge in that year (Fig. 5.2). Isotopic values for the two birds with trackers were $\delta^{15}N$ = 6.99 and 7.62‰ and $\delta^{13}C$ = 25.71 and 25.21‰, similar to mean values recorded for Antarctic petrels, a species that forages exclusively within Antarctic waters (Hodum and Hobson, 2000).

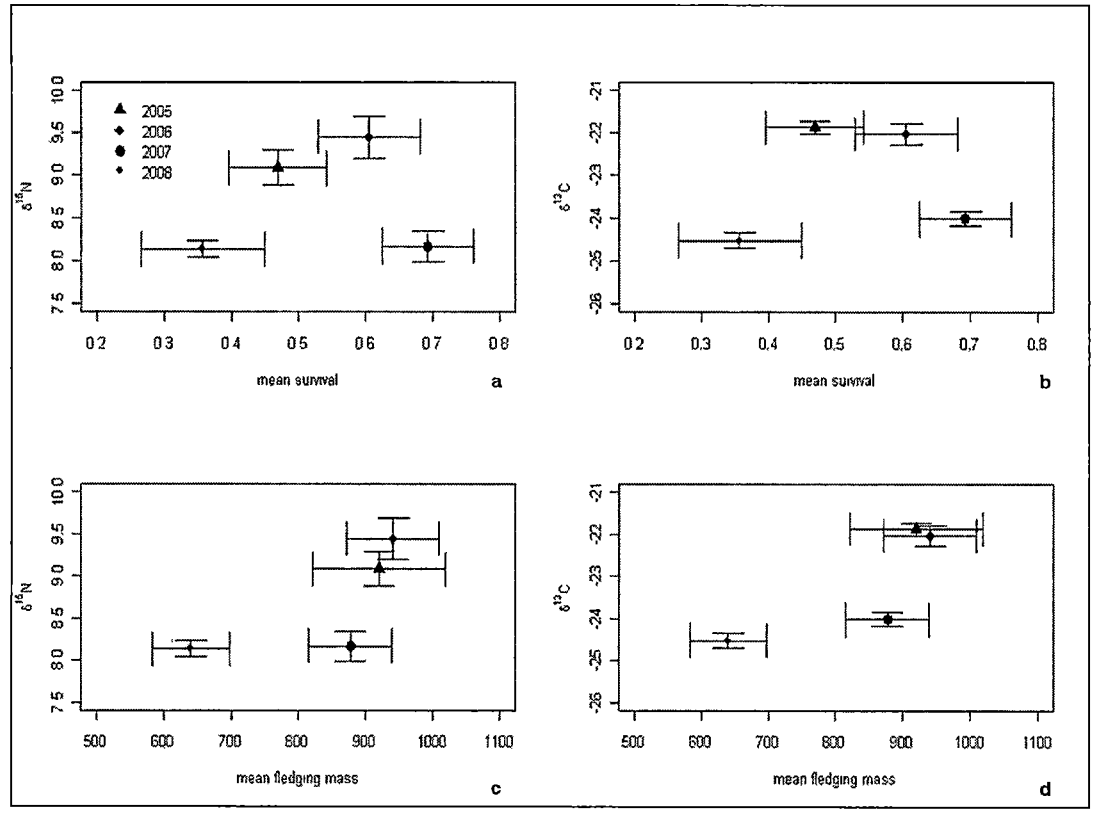

Fig. 5. 1. a) Stable isotopic ratios of Nitrogen ($\delta^{15}N$) and survival of chicks (n = 498) between the austral summers of 2005–08 inclusive; b) Stable isotopic ratios of Carbon ($\delta^{13}C$) and survival of chicks (n = 498); c) Stable isotopic ratios of Carbon ($\delta^{13}C$) and fledging mass of chicks (n = 57); and d) Stable isotopic ratios of Nitrogen ($\delta^{15}N$) and fledging mass of chicks (n = 57). Error bars represent the standard errors for all values.

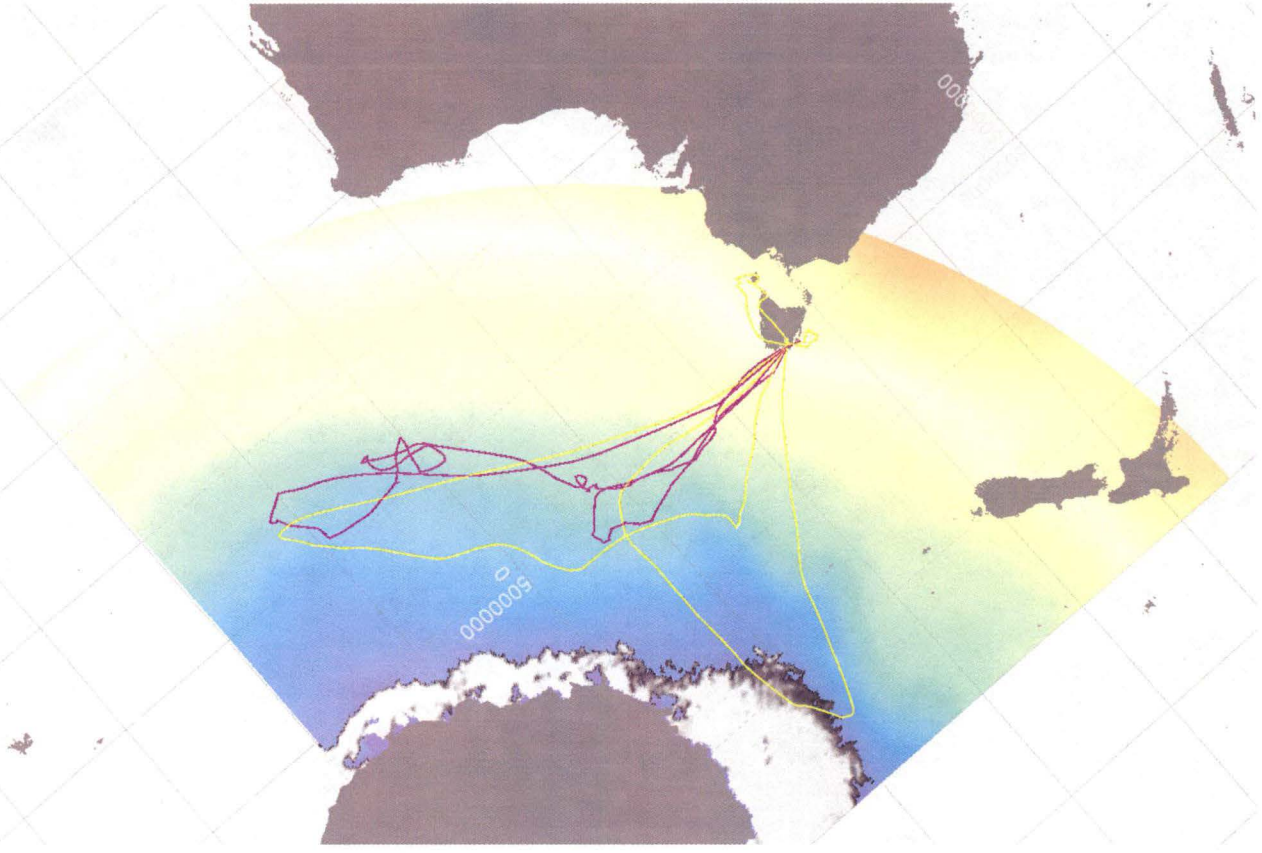

Fig. 5. 2. Tracks for two short-tailed shearwaters with loggers deployed on 17th January 2008 and retrieved on 15th March 2008. Five individual long foraging trips of between 11 and 19 days are shown against mean ice-edge extent and mean sea-surface temperature for late February, early March 2008.

Isotope analysis

Nitrogen signatures ranged from 6.9 to 11.83‰ (Table 5.2) representing a 1–2 trophic range in the trophic position of prey items. Carbon values ranged from -19.69 to -25.87‰ representing a wide range in food source location from inshore coastal foraging near the coast of Tasmania to offshore Antarctic foraging. Cluster analysis divided the samples into two groups, influenced by inter-annual differences in both trophic foraging level and latitudinal prey distribution (Fig. 5.3). Of the 89 samples in group 1, 85 of these occurred during the 2004–05 and 2005–06 seasons (Table 5.3) and this group was indicative of higher trophic feeding ($\delta^{15}N$ range = 7.8–11.56‰) with $\delta^{13}C$ signatures representing assimilation of nutrients closer to shore ($\delta^{13}C$ range = -23.8 to -19.7‰). In previous studies on penguins (with a smaller spatial distribution than short-tailed shearwaters), the upper range of the carbon signature that we recorded is similar to that reported for northern rockhopper penguins (*Eudyptes chrysocome moseleyi*) which forages in sub-tropical waters (Cherel & Hobson 2007). During the latter seasons, 128 of 154 observations occurred within group 2. Group 2 comprised isotopic signatures more typical of lower trophic foraging in Antarctic waters with values ($\delta^{15}N$ range = 6.9–10.95‰, ($\delta^{13}C$ range = -25.9 to -22.0‰) similar to a number of petrel species that forage exclusively within the Antarctic (Hodum & Hobson 2000). We did not detect any within season differences in trophic level or foraging location.

Table 5. 2. δ15N and δ13C signatures (means ± SD and range) for whole blood of short-tailed shearwaters, *Puffinus tenuirostris* over three stages of the breeding season for four successive years, n= number of birds.

year	stage	date	$\delta^{15}N$ (‰)	range $\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	range $\delta^{13}C$ (‰)	n
2005	incubation	15/01/2005	8.80 ± 0.54	7 80 to 9.71	-21.92 ± 0.43	-22 76 to -21.24	23
	early chick	10/02/2005	8.82 ± 0.64	7.95 to 9.84	-21.41 ± 0.50	-22.14 to -20.57	9
	late chick	10/02/2005	9 72 ± 0.54	8.73 to 10 82	-22 09 ± 0.49	-22.88 to -21.14	14
2006	incubation	14/01/2006	9.79 ± 0.70	8 7 to 11 56	-22 45 ± 0.60	-23 32 to -21.41	21
	early chick	5/02/2006	9.97 ± 0 80	8.78 to 11.83	-21.15 ± 0.66	-22.25 to -19.69	25
	late chick	5/03/2006	8 36 ± 0 39	7.51 to 8.99	-22 74 ± 0.59	-23.84 to -21.658	19
2007	incubation	14/01/2007	7.79 ± 0 46	7 03 to 8 62	-24.11 ± 0.51	-25.24 to -23.25	24
	early chick	16/02/2007	8.6 ± 0.93	6.90 to 10 95	-24.25 ± 0.76	-25.87 to -23.08	22
	late chick	16/02/2007	8.16 ± 0.43	7.13 to 8.99	-23.63 ± 0.63	-24.8 to -22.023	20
2008	incubation	16/01/2008	8.24 ± 0.40	7.49 to 8.92	-23 89 ± 0.55	-24 71 to -23.07	21
	early chick	15/02/2008	8.15 ± 0 30	7.55 to 8.81	-24.78 ± 0.51	-25 79 to -23.59	25
	late chick	15/03/2008	8 01 ± 0.44	6 99 to 9.07	-24 84 ± 0.54	-25 71 to -24.15	20

Table 5. 3. Month and year identification of similarity matrix groupings.

	incubation		early chick rearing		late chick rearing		
group	**1**	**2**	**1**	**2**	**1**	**2**	**n**
2005	20	3	9	0	13	1	46
2006	12	9	25	0	6	13	65
2007	0	24	3	19	1	19	66
2008	0	21	0	25	0	20	66
n	32	57	37	44	20	53	**243**

Inter-annual differences were clear when compared to other seabird predators (Fig. 5.4). Samples from group 1 shared similar $\delta^{15}N$ values to the Antarctic petrel (an intermediate forager of crustaceans and fish) and $\delta^{13}C$ values to those of the king penguin (Cherel et al. 2007), suggesting sub-Antarctic foraging. Short-tailed shearwater chicks whose isotopic signature is generally representative of higher trophic food obtained in neritic waters than the adult diet (Cherel et al. 2005) also overlapped with $\delta^{15}N$ and $\delta^{13}C$ values suggesting foraging within Australian shelf and coastal waters. Samples from group 2 shared similar $\delta^{15}N$ values with the crustacean-feeding Adelie penguin (Cherel 2008) and similar $\delta^{15}N$ and $\delta^{13}C$ to the Antarctic petrel, a species that forages exclusively within waters surrounding the Antarctic continent, generally feeding on crustaceans and fish. There was considerable variation with the Carbon values of shearwaters in this group, suggesting variability in individual foraging which can also be observed on the tracks of the birds (Fig. 5.2).

The mixing model incorporated known prey species from the diet of short-tailed shearwaters sourced from previous studies using stomach sampling, stable isotope and fatty acid analysis (Skira 1986; Cherel et al. 2005; Connan et al. 2005) (Fig. 5.5). The possible prey breakdown, when categorised by the two groups identified in the cluster analysis, demonstrated two distinct feeding scenarios. Firstly, estimates of diet from the mixing model during 2004–05 and 2005–06 were mostly post-larval fish and the subantarctic Euphausiid, *Euphausia vallentini* with minor contributions from the hyperiid amphipod *Themisto gaudichaudii* and the arrow squid *Notodarus gouldi.* Secondly, group 2, more prevalent in 2006–07 and 2007–08, was dominated by Antarctic Krill (*E. superba),* squid (*Psychroteuthis*

glacialis), Antarctic silverfish (*Pleuragramma antarcticum*) with some contribution from the sub-Antarctic species, *E. vallentini.*

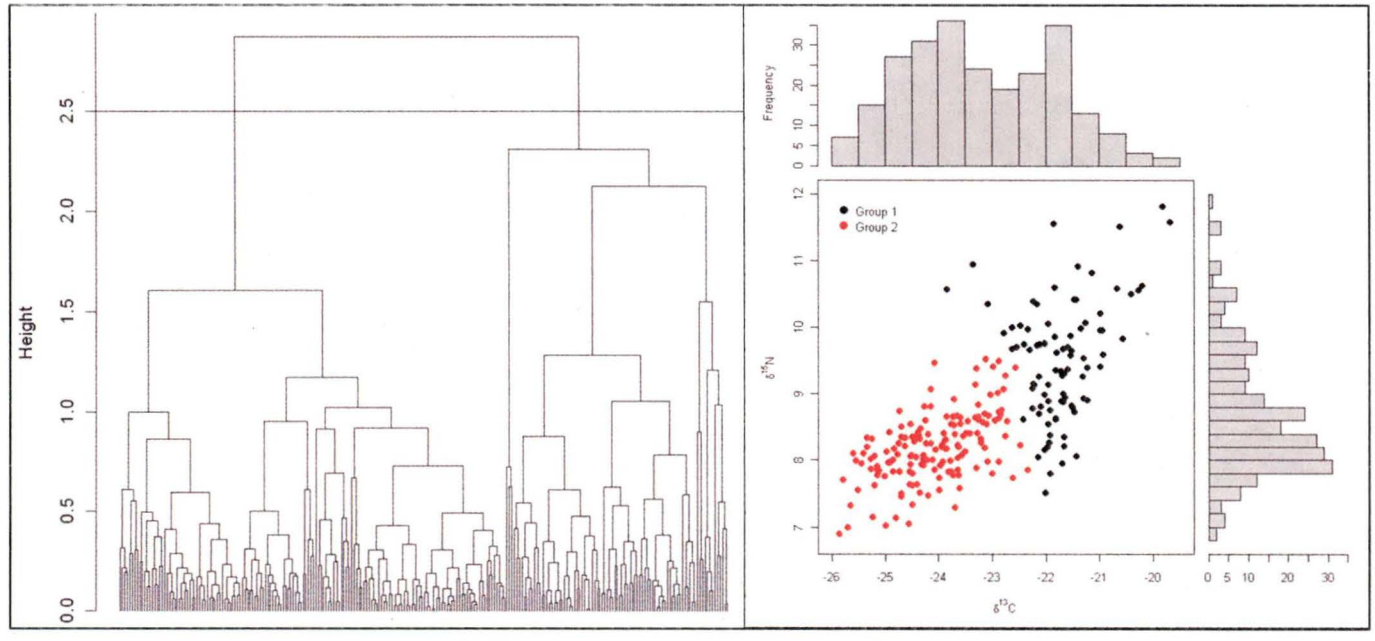

Fig. 5. 3. a) dendrogram (Bray-Curtis similarity matrix groupings) for δ15N and δ13C of 243 blood samples of short-tailed shearwaters collected between the austral summers of 2005 and 2008 inclusive; and b) scatterplot for $\delta^{15}N$ and $\delta^{13}C$ of 243 blood samples with marginal histograms according to groupings identified by cluster analysis.

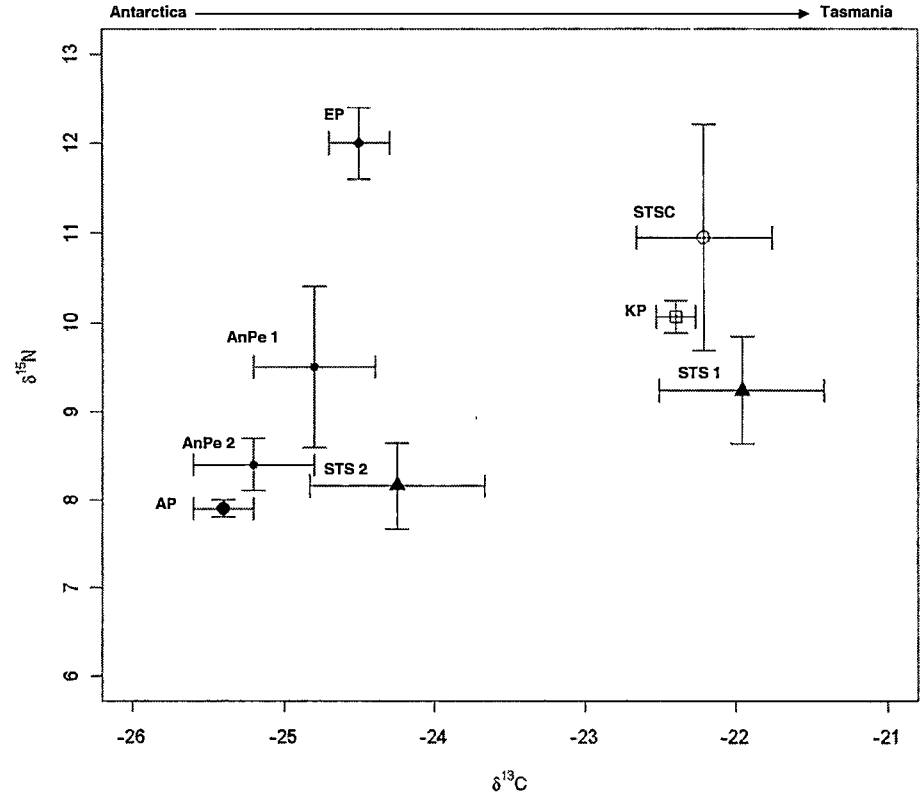

Fig. 5. 4. Stable isotopic ratios of Carbon (δ13C) and Nitrogen (δ15N) for whole blood of adult seabirds. Estimated foraging locations are indicated at the top of the panel. EP, Emperor penguin; AP, Adelie penguin (Cherel 2008); **KP, king penguin** (Cherel et al. 2007), **STS 1 and STS 2, short-tailed shearwaters (group 1 and group 2 respectively, this study); AnPe 1, AnPe 2, Antarctic petrel (1994–95 , 1995–96 respectively,** (Hodum & Hobson 2000) **and STSC, short-tailed shearwater chick from plasma** (Cherel et al. 2005).

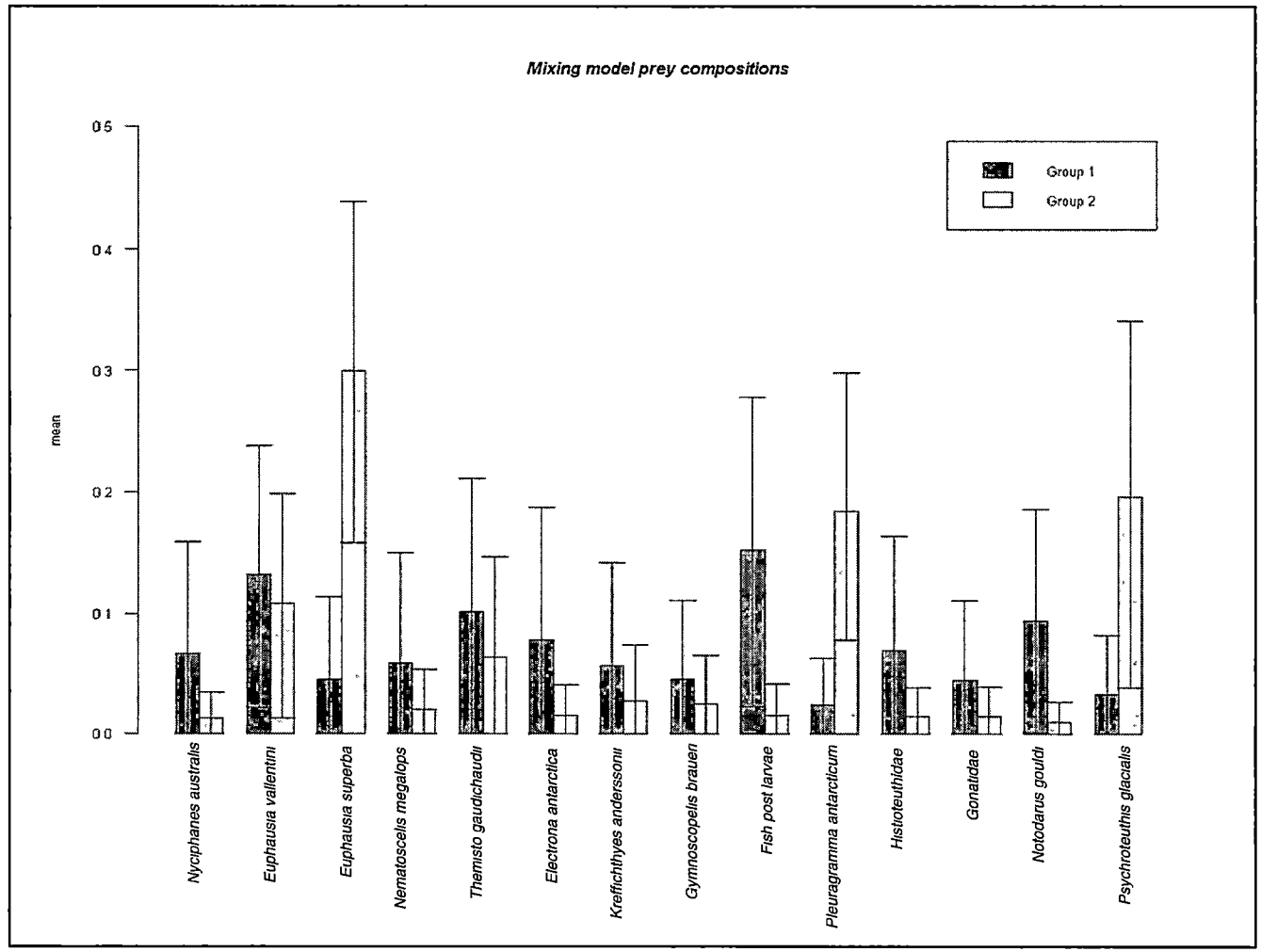

Fig. 5. 5. Mixing model estimates of prey consumption according to groupings identified by cluster analysis. Error bars represent standard errors.

Discussion

Obtaining information on the temporal and spatial variability of diet in seabird predators contributes to understanding the interactions between seabirds and their biotic environments (Tierney et al, 2008). However, traditional methods of obtaining diet such as stomach sampling have precluded the identification of prey items in species that undertake long foraging trips in remote oceanographic regions. This is because stomach samples are only indicative of prey consumed within a short distance of the breeding colony and can be biased towards less digestible prey (Quillfeldt et al. 2005). Subsequently there are gaps in knowledge about prey consumption in wide-ranging seabirds and how they respond to changes in food supply and distribution. Stable isotope analyses revealed plasticity in the foraging behaviour of short-tailed shearwaters with clear inter-annual differences in diet during the four years of the study that did not necessarily affect reproductive performance.

Diet composition as inferred by SIA

The 2004–05 and 2005–06 breeding years demonstrated Nitrogen signatures similar to those of the Antarctic petrel, a species that consumes both crustacean and fish prey with an isotopic signature intermediate between these prey items (Arnould & Whitehead 1991; Hodum & Hobson 2000). Previous analysis of short-tailed shearwaters by Cherel et al. (2005) reported proportions of up to 87% myctophid fish in the diet. The Nitrogen isotopic signatures reported here are lower than would be expected if the diet was mainly myctophids, as the signatures were less than those reported for king penguins who forage almost exclusively on these prey (Cherel et al. 2007) (Fig. 5.4). Indeed, the possible feeding scenario proposed by the Bayesian mixing model, inferred that the diet was comprised of fish post-larvae and *E. vallentini* which is similar in composition, if not proportion, to the results reported by Cherel et al. (2005) of short-tailed shearwaters from the breeding season of 1996–97.

The 2006–07 and 2007–08 breeding seasons demonstrated a distinct diet shift and Nitrogen values were much lower than in the previous breeding years showing

more consistency with Adelie penguins and Antarctic petrels, both of whom have been reported as containing high levels of crustaceans in their diet (Hodum & Hobson 2000; Tierney et al. 2008). The Bayesian mixing model for this group provided a scenario with diet dominated by lower trophic prey, *E. superba, E. vallentini, Psychroteuthis glacialis* and *Pleuragramma antarcticum* (Fig. 5.5) with the exception of *Pleuragramma antarcticum.*

Foraging locations as inferred by SIA and geo-location

Carbon signatures during the 2004–05 and 2005–06 breeding years were similar to those previously reported for short-tailed shearwater chicks (Cherel et al 2005). Chick blood isotopic values are considered to be a direct representation of resources close to the breeding colony as they represent diet obtained during short-trips of adult birds (Weimerskirch & Cherel, 1998). This is in comparison to adult isotopic signatures that are more representative of long trips due to the turnover of isotopes in whole blood (Forero & Hobson 2003). Similar adult Carbon values to chick Carbon values would indicate that adult birds in these years were exploiting resources quite close to the breeding colony but values also overlapped with king penguins who forage within the polar front (PF) and polar frontal zones (PFZ) (Cherel et al. 2007) suggesting that foraging occurred over a wide range of water masses from the Tasmanian coastline to polar waters. In contrast, the 2006–07 and 2007–08 breeding years displayed Carbon signatures that overlapped with Antarctic petrels in 1994–95 and with emperor penguins (Hodum & Hobson 2000; Cherel 2008). Both are exclusively Antarctic species and forage within water masses surrounding the Antarctic continent which would infer that in these later years, adult short-tailed shearwaters in this study were foraging almost exclusively in Antarctic waters during long trips. This was demonstrated by geo-location for the 2007–08 breeding year which showed that birds during chick rearing were foraging at the ice-edge extent in long trips lasting about 14 ± 2 days (Fig. 5.2).

This was an important finding as it has been recognised that due to the foraging range of short-tailed shearwaters and the temporal scale associated with measuring stable isotopes in whole blood, Carbon values are likely to

underestimate the southern and northern limits of foraging with the resulting values being intermediate between the extremes of foraging distribution (Cherel et al. 2005). Due to the turnover in whole blood of three to four weeks any sample taken during chick rearing (when the birds return to the nesting site) is likely to incorporate 1–2 long trips (14 ± 2 days) and three or four days of short trips. In some cases, sampling may occur during a series of short trips which may result in a more intermediate estimate of foraging limit than those taken upon return from a long trip. However, the majority of prey incorporated will be from long trips and we have demonstrated that the Carbon values obtained from the logged birds support the geographic information that showed birds foraging within and below the PFZ. This would indicate that the southern extremities are not being underestimated in this case and that there was a geographic and trophic diet shift that occurred in 2007 and 2008.

Inter-annual differences in diet relative to reproductive performance

The measurement of reproductive success in tandem with inference methods provides the direct impact of resource availability i.e. via survival of offspring (Pat Herron Baird 1990; McMahon et al. 2009). The diet shift in both trophic level of prey consumption and geographic foraging location was not directly linked to the survival or fledging mass of chicks during the four years of the study. Chick survival and mean fledging mass varied between years, independently of the isotopic signature. Of particular interest was the contrast between 2006–07 and 2007–08 as both displayed similar blood isotopic signatures (implying a similar adult diet for both breeding years), however, survival and fledging mass were significantly lower in 2008 than in 2007. This identifies one of the limitations in stable isotope analysis: isotopes can identify trophic level and approximate geographic location but cannot provide information on prey abundance.

The significance of the shift in diet may be related to the Match-Mismatch Hypothesis (MMH). This hypothesis, although originally formulated for fisheries (Cushing 1969) has recently been related to higher trophic marine predators (Durant et al. 2007). It states that if peak energetic requirements occur at the same time as peak prey productivity, recruitment and success will be high (match),

whereas if peak energy requirement occurs at a low peak prey productivity, then recruitment or success will be low (mismatch) (Durant et al. 2007). Prey abundance is also of significance as prey may be matched in timing but reduced in abundance. Or, prey may be mismatched in timing but high in abundance, both of which can disrupt or amplify the classic MMH scenario (Durant et al. 2007). MMH offers a useful way to interpret the differences in vital rates we observed. In the 2008 season we may have observed either the former scenario where timing was matched but abundance was low or a mismatch in timing of peak production, resulting in lower overall survival and chick mass. This may have occurred either inshore (related to direct resource availability for chicks) or offshore (adult body maintenance and some chick resource allocation). The ability to isolate the influences on lowered survival and fledging was reduced however, by sampling only adult birds. As adult samples represent the assimilation of prey during long foraging trips (Weimerskirch & Cherel 1998), we were unable to infer any information about resources close to the breeding colony and subsequently their direct effects on chick survival and fledging mass. Any future research on this breeding colony should incorporate chick samples.

Flexibility in foraging strategies

Long trips in species that employ a bimodal feeding strategy are used to improve adult body condition by exploiting distant resources (Weimerskirch & Cherel 1998). However, birds will still maximise their fitness while reducing energetic costs (Jonsson 1997). The foraging strategies of top predators will evolve in response to the temporal and spatial distribution of prey, and for opportunistic feeders, this often manifests as flexible foraging behaviours. Behavioural foraging patterns demonstrated by short-tailed shearwaters include Area-Restricted Search (ARS) to increase their prey encounter rate in response to patchily distributed prey (Kareiva & Odell 1987; Weimerskirch et al. 2007), straight line search (Zollner & Lima 1999; Weimerskirch et al. 2007) and foraging site fidelity (Bradshaw et al. 2004).

Prey availability, prey abundance and the subsequent response of predators, are ultimately dictated by oceanographic characteristics. The Southern Ocean has demonstrated changes in the distribution of water masses, including a movement

of the PF and southern Antarctic circumpolar current front (SACCF) of up to 60 km south in the last decade. This may increase the foraging effort and decrease the reproductive success of some predators (Inchausti et al. 2003) and for central place foragers such as short-tailed shearwaters, any increase in distance to a foraging zone effectively reduces food availability, owing to an increase in travel time (Durant et al. 2005). Conversely, the shift in fronts may decrease foraging effort and increase reproductive success of some predators, as it has been postulated that climate change may increase the occurrence rate of temporal mismatch. This may affect overall primary productivity which will in turn increase food abundance (Durant et al. 2005). The direction this will manifest is as yet unknown. It may vary between the two extremes which would result in a reproductive success rate similar to that observed in our study. Shearwaters are highly mobile and can forage over a wide geographic range without significant increases in foraging effort (Weimerskirch & Cherel 1998). This allows them to negotiate small-scale changes in prey availability during the chick rearing period. Despite observing plasticity in their foraging behaviour that may make them resilient to increasing environmental variation during chick rearing, the continuing decline of short-tailed shearwaters on Wedge Island (Chapter 2) would suggest that there may be other critical temporal or spatial scales in their life-history at which behavioural modes are inadequate to ensure continued adult survival.

Acknowledgements

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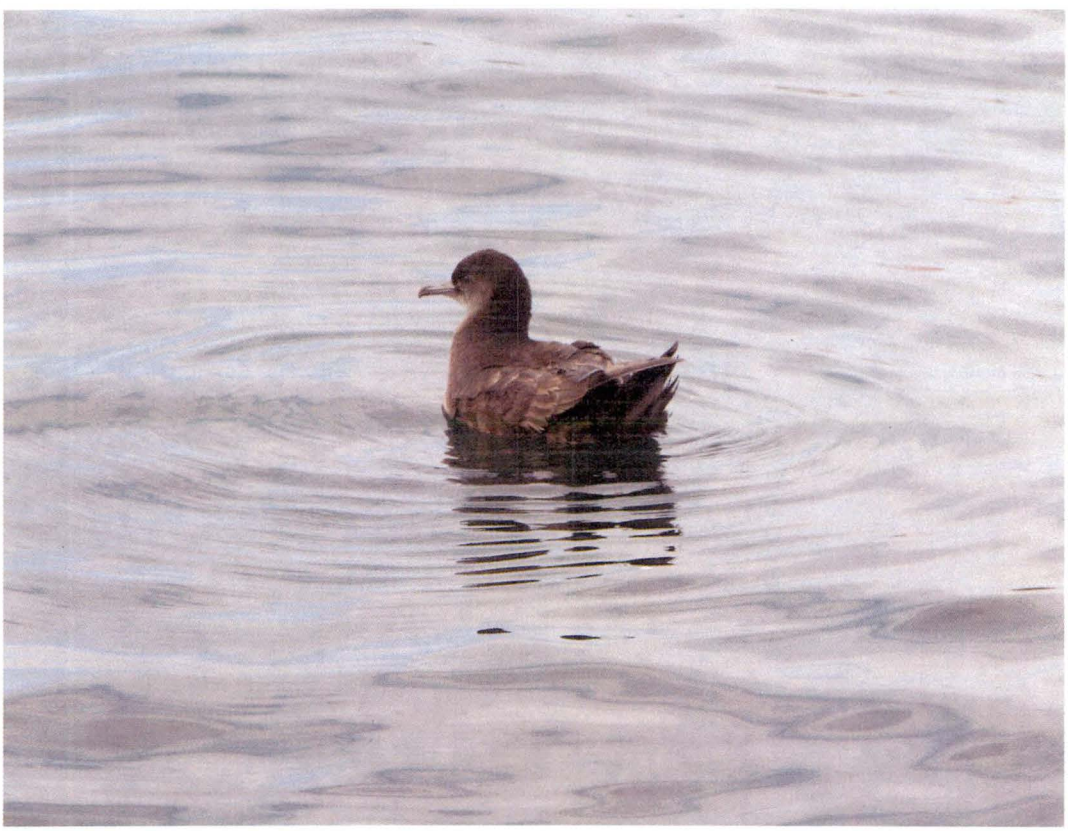
Chapter 6



Chapter 6

Detecting trends between environmental variation and the population trends of short-tailed shearwaters (*Puffinus tenuirostris*) in south-east Tasmania

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Abstract

The biological responses of Southern Ocean predators to environmental variation are expected to vary greatly in relation to a number of factors including the magnitude and temporal longevity of the change. We examined the relationship between an exponential rate of change of –15% over 7 years on the rate of egg laying and survival of chicks of a population of short-tailed shearwaters on Wedge Island with physical oceanographic variables. Tested variables included sea surface temperature (SST), Chlorophyll a (Chla) as a proxy for primary productivity, wind speed and direction, sea surface height (SSH), sea surface height anomaly (SSHa) and ice-edge extent. Trends were identified using linear models (lm) and generalised linear models (GLM). In order to further refine the possible effect of variation in these variables, the analysis was broken down to three spatial scales (inshore foraging limit, offshore foraging limit and winter feeding grounds) and three temporal scales (wintering, pre-egg laying and chick rearing). While no relationships were determined between chick survival and environmental variables, we detected a relationship between a decline in egg

laying and an increase in pre-egg laying sea surface height anomaly (SSHa) in the Southern Ocean. Determining specific biological mechanisms for how increasing SSHa may affect prey availability and abundance, and therefore the population demography of shearwaters, is difficult. However, indications are that large scale oceanographic change may be negatively affecting the population demography of one of the most abundant seabirds in the Southern Hemisphere.

Introduction

The nature of relationships between physical and biological processes is subtle and complex. This is because not only do physical processes define structures within which biological processes occur, but they also influence the rate of biological processes indirectly via energy flow (Mann & Lazier 2006). Physical processes within the marine environment are driven by climate effects which may be cyclical, such as El Nino Southern Oscillation (ENSO) events, or the Pacific Decadal Oscillation (PDO). These may be short or long-term in duration. Climate variation may also be anthropogenically driven and there is an increasing body of evidence to suggest that the Southern Ocean (which plays a critical role in global climate patterns) has been exhibiting increased variation in physical oceanographic parameters during the last 50 years (Gille 2002; Levitus et al. 2005; Rignot et al. 2008).

The biological responses of predators to environmental variation, via the regulation of resources available to animals, are as yet poorly understood as no single index can provide all the information (Piatt et al. 2007). The responses of predators are wide ranging and can encompass direct effects (*e.g.* increased adult mortality resulting in population declines and/or changes in phenology) or lagged effects (*e.g.* increase or reduction in breeding success). Also these effects may vary greatly in relation to the magnitude and temporal longevity of variation, and the effects may be species specific (Inchausti et al. 2003; Durant et al. 2007; Tremblay et al. 2009; Nevoux et al. 2010). Therefore, understanding the level of changes, involves collating information on multiple species from different regions that forage at different trophic scales as this provides the linkages for describing changes in population demography of predators.

A number of recent studies have related population demographics, at-sea observations and abundance of seabirds to environmental variables (for a review of the latter see Tremblay et al. 2009). For example, links have been identified between:

1. Laying date and sea-surface height in Cassin's auklet (*Ptychoramphus aleuticus*) (Wolf et al. 2009);

2. Foraging behaviour and primary productivity in red-footed boobies (*Sula sula*) (Weimerskirch et al. 2005);
3. Foraging and association with fronts in multiple species (Hyrenbach et al. 2006);
4. Timing of breeding and winter North Atlantic Oscillation (wNAO) in guillemots (*Uria aalge*) (Votier et al. 2008);
5. Survival and sea-surface temperature in multiple species (Sandvik et al. 2005);
6. Breeding success and sea-ice extent in emperor and Adelie penguins (*Pygoscelis adeliae*) (Barbraud & Weimerskirch 2001; Emmerson & Southwell 2008; Beaulieu et al. 2009);
7. Breeding success, chick survival and wind speeds and sea-ice extent in Wilson's storm petrel (*Oceanites oceanicus*) (Quillfeldt 2004); and
8. Foraging and sea-surface height anomalies in grey-headed albatross (*Thalassarche chrysostoma*) (Nel et al. 2001).

Hence studies of seabirds are providing end results of changing environmental conditions while increased availability of remote sensing oceanographic data is helping to provide information on the mechanisms that may be driving these changes.

There is considerable information relating population parameters such as breeding effort, foraging efficiency and survival to short term effects (from one season to another). However, long-term effects of environmental variation are generally more complex and difficult to appreciate (Nevoux et al. 2010). While some environmental variables such as sea-ice extent have been recorded for decades, other variables such as sea-surface height (SSH), sea-surface height anomaly (SSHa) and primary productivity have only been available since the 1990s. This presents problems when assessing trends in these oceanic variables, as the time-series available are often not long enough to detect long-term trends and therefore relate those trends to their effects on population demography. Despite long-term data series on the breeding biology of some seabird predators, most studies attempting to link breeding variables with oceanic variation are dealing with limited

data sets (Beaulieu et al. 2009) which may reduce the power of overall conclusions.

Short-tailed shearwaters (*Puffinus tenuirostris*) are among the most abundant Southern Ocean seabirds. They are long-lived, and have low reproductive output. Consequently, populations are particularly vulnerable to changes in adult survival (Bradley et al. 1991), whereas changes in juvenile survival may take years to appear in a breeding colony owing to delayed maturation rates. They are highly synchronous breeders and migrate from the Bering Sea during the austral winter to their breeding colonies in southern Australia. Once they return to the breeding colonies, the adult birds undertake a 'honeymoon' trip to the Southern Ocean in order to re-establish body condition lost during the migration (Weimerskirch & Cherel 1998). The majority of the information on breeding short-tailed shearwaters has been gained from colonies that are in the centre of the species distribution (Bass Strait Islands). However, current long-term trends remain largely unpublished.

A recent study of short-tailed shearwaters at the southern most extremity of their breeding distribution has reported a reduction in the number of birds laying eggs each year since 2003, with an exponential rate of change of –15% per annum (Chapter 2). A series of hypotheses such as investigator disturbance, onshore habitat characteristics and recreational poaching of nearly-fledged chicks were ruled out as contributing to the decline. A number of hypotheses remain with some unable to be tested given the current constraints of the study (including source-sink population dynamics, decline in habitat quality and incidental mortality from fisheries by-catch).

As long-lived seabirds may incur survival costs resulting in a trade-off between adult survival and breeding investment (Golet et al.1998) and may be associated with specific large and meso-scale oceanographic features (Hyrenbach et al. 2006) it follows that there is a spatio-temporal scale at which trade-offs may occur. Given the rapid exponential rate of change (–15% per year) observed in short-tailed shearwaters on Wedge Island during the past 7 breeding years, the aim of this study was to test the effects of multiple environmental variables on the rate of

egg laying and chick survival. Information about the specific foraging ranges of Wedge Island short-tailed shearwaters that are specific to critical stages in breeding was used in order to look for correlates with the decline in breeding birds.

Methods

Field work was conducted on Wedge Island in south-east Tasmania, Australia (43° 07' S, 147° 40' E). This island was selected due to its position at the periphery of the breeding distribution of short-tailed shearwaters. Most studies on these animals have focused on the Bass Strait Islands which is the centre of the distribution and yet reductions in breeding numbers are usually primarily detected from the edges of breeding distributions first (Wilcove & Terborgh 1984). In brief, transects were laid across the island 25 m apart for 500 m from the northern tip and 50 m apart thereafter to the southern end of the island (total length of island 1250 m, 35 transects). Quadrats were placed 20 m apart on transects 1–20 and 25 m apart on transects 15–35 (with transects 30, 31 and 32 removed from the study due to their fragility) and a total of 641 burrows within these quadrats were marked and checked in December and April between 2003 and 2009. Detailed methodology for the collection of egg-laying and reproductive data is detailed in Chapter 2.

Rate of egg laying and survival of chicks

Methodology for the calculation of egg laying rates is detailed in Chapters 2 and 3. To produce a model set with which to measure these life-history traits against environmental variables, egg laying and chick survival were summarised on an annual basis which resulted in an effective sample size of n = 7 for egg laying and n = 6 for chick survival. This is a small-time series with which to identify trends, particularly in a long-lived seabird that may breed for up to up to 27 (mean = 15) years after entering the breeding colony (Bradley et al. 1989). Therefore, while we can be confident that the detection of a significant trend in egg laying is a real observation, this sample size may underestimate any non-significant results (Gerard et al. 1998) in the analysis of chick survival which should then be interpreted cautiously. A generalised linear model (GLM) was used to compare

the mean survival rate of chicks between years to look for corresponding trends with the rate of egg laying. Rates of chick survival using the entire data set (as opposed to means) were then compared between years using a generalized linear mixed effects model (glmer) in R using the lme4 package (Bates & Maechler 2009) in order to determine if years were significantly different from each other. Chick survival (fledge) and year were designated as fixed effects, quadrat was included as a random effect and Laplace approximation was used to estimate model fit.

Identification of spatial foraging characteristics

Short-tailed shearwaters forage over a wide range during their breeding season and have previously been reported to exploit waters as far as the Antarctic ice-edge extent (Weimerskirch & Cherel 1998; Woehler et al. 2006). In order to ascertain specific locations of foraging importance, geo-location devices were deployed in the 2007–08 season (detailed in Chapter 3). The tracking data were used to define boundaries for offshore foraging (62–45° S, and 100–175° E) and inshore foraging (38–45° S and 142–152° E) (Fig. 6.1). As breeding is dependent on adult body condition (Erikstad et al. 1998), the winter foraging grounds were also considered in this study with an approximate foraging range taken from Shaffer et al. 2006 in a study on the closely related sooty shearwater, *Puffinus griseus* that are reported to exploit the same areas during the austral winter (Wahl et al. 1989). The winter foraging range was defined as 160° E–120° W and 35–65° N (Fig. 6.1) although we recognise that due to the association of birds with meso-scale events (Hyrenbach et al. 2006), and the foraging site fidelity shown by short-tailed shearwaters in the Bering Sea (Baduini et al. 2006) that this spatial scale is large and trends are likely to be underestimated in this region.

Identification of temporal foraging characteristics

The most prominent life-history trade-off involves the cost of reproduction. It has two major components, costs paid in survival and costs paid in future reproduction (Stearns 1989). Therefore the ultimate cost for any breeding animal is its own survival. Short-tailed shearwaters, like many *K* selected species have high adult survival of 93% (Bradley et al. 1989). However, there remain three critical stages

of breeding effort present at which the trade-off between adult survival and reproduction can occur:

1. Wintering. Where adults do not return to the breeding colonies due to mortality during migration (defined here as May 1 to Aug 20, the bulk of the winter season);
2. Pre-egg laying. Where body condition is insufficient to begin a breeding attempt (defined as September 21, the average return date to the breeding colony to November 27, the mean laying date); and
3. Chick rearing. This is the most energetically expensive period of breeding (Woehler et al. 2006) and failure may occur from either adults abandoning the attempt due to their own body condition or from adults not supplying enough food to their offspring (defined as Jan 10, mean hatching date, to March 20, approximate time of adult birds leaving for migration). Chick rearing was further divided for some variables to early chick rearing (10 Jan to 01 Feb) and late chick rearing (02 Feb to 20 March).

This provided a spatio-temporal frame that is specific to the Wedge Island colony of birds in order to test against various oceanographic variables.

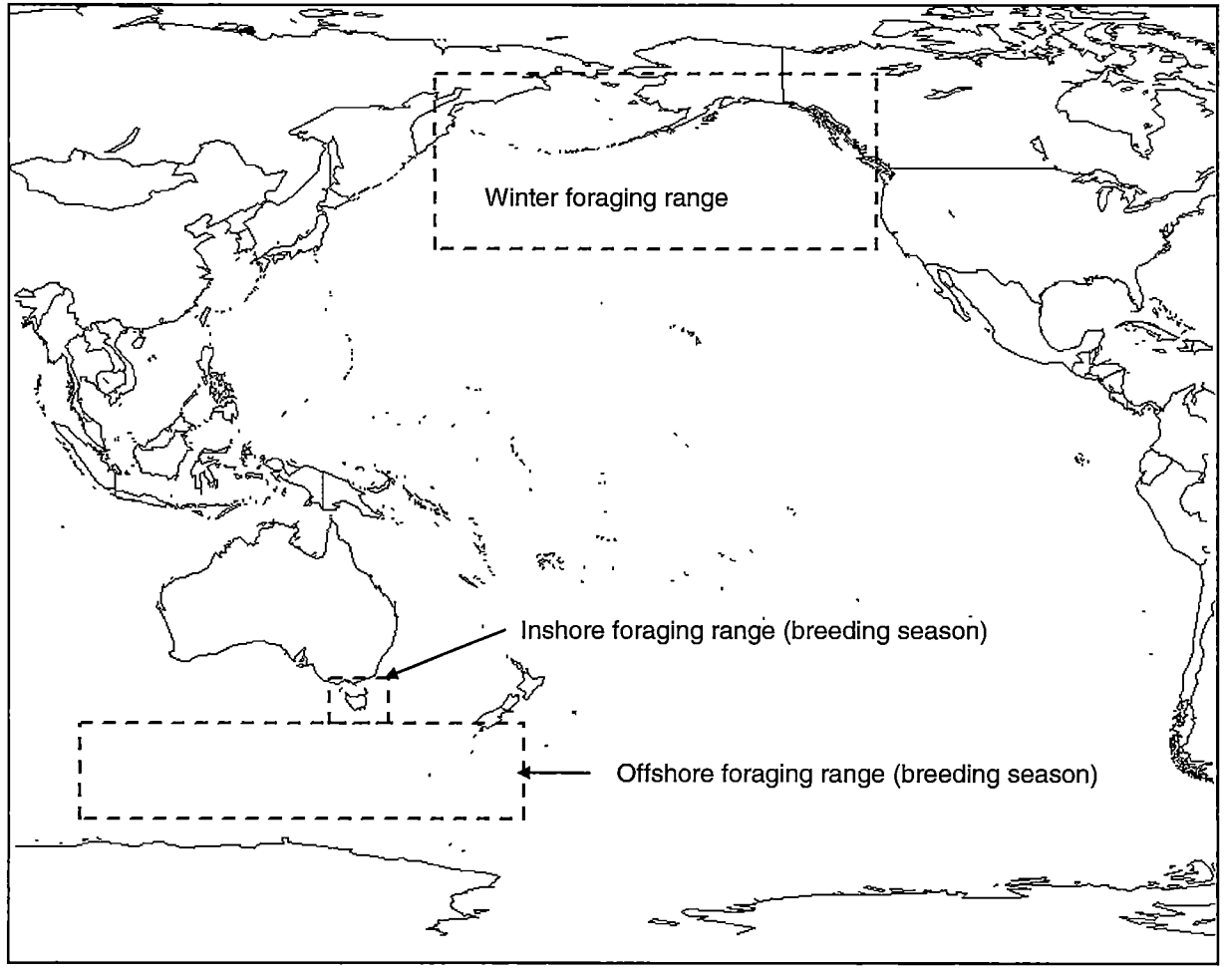


Fig. 6. 1 Foraging locations of short-tailed shearwaters during the austral summer and winter.

Selection of environmental variables

The following oceanographic variables were isolated for each spatio-temporal scale to test for correlations with the rate of egg laying and chick survival:

1. Sea surface temperature (SST), reflecting heat content of the uppermost layer of the ocean (NOAA_OI_Sea-surface temperature (SST)_V2 SST data (monthly; 1-degree resolution)), were obtained from the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html));
2. Surface chlorophyll-a data (8-day composites, 9 km spatial resolution), as a proxy for primary productivity, were obtained from SeaWIFS and MODIS Aqua satellite estimates (Feldman & McClain 2010);
3. Sea surface height and sea surface height anomaly data (7-day resolution; $^1/_3$-degree spatial resolution), which integrates heat content of the water column at all depths as well as current flow (Wolf et al. 2009), were obtained from http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/index.html;
4. Ice-edge extent, which may alter prey distribution and available foraging area (Beaulieu et al. 2009) were obtained from the Australian Antarctic Data Centre (IDN Node AMD/AU) (Raymond 2009);
5. Estimates of winds at 10 m altitude which may influence foraging effort and upper level water mixing, were obtained from NCEP/NCAR reanalysis data (Kalnay et al. 1996). These data were treated as meridional and zonal components, and also combined into overall wind speed and direction values; and
6. Southern-Oscillation index was obtained from the Australian Bureau of Meteorology (BOM) http://www.bom.gov.au/climate/current/soihtm1.shtml.

For variables 1–5, the mean value of each pixel over the period of interest was first computed. The mean and standard deviation (SD) of those values was then calculated within the region of interest to give indicators of the spatial mean and variability. The SD of each pixel over the period of interest was also calculated, and then averaged within the region of interest to obtain an indication of the within-

period temporal variability. Chlorophyll-a values were log-10 transformed prior to calculation of means and SDs; SDs were not calculated for wind directions.

Measuring trends in ocean data

As we observed a strong exponential rate of change of –15% in the rate of egg laying, we reasoned that the best measures of influence on the trend in breeding birds would be corresponding trends in the oceanographic variables. Identifying these trends would allow simplification of the model set by excluding variables that were not likely to be biologically relevant prior to analyses. To test for corresponding rates of increase, we used linear models (with Gaussian error distributions) of oceanographic variable and year. Data were examined for trends, and time scales varied from 29 years (sea-ice extent) to 8 years (Chlorophyll a) (Table 6.1). We then investigated correlation between the environmental variables using Pearson's product moment correlation coefficient.

Table 6. 1. Linear model results for oceanographic variable, temporal and spatial region, F statistic (df) and p values. Significant results are in bold.

Variable	temporal/spatial region	Years	F	p
Sea surface temperature	Pre egg laying/inshore	1998-2009	0.66 (1, 10)	0.400
Chlorophyll a	Pre egg laying/inshore	1998-2009	0.38 (1,10)	0.550
Sea surface height	Pre egg laying/inshore	2000-2008	0.61 (1,8)	0.459
Sea surface height anomaly	Pre egg laying/inshore	2000-2009	0.58 (1,8)	0.468
Zonal wind	Pre egg laying/inshore	1998-2009	0.51 (1,10)	0.492
Meridional wind	Pre egg laying/inshore	1998-2009	0.34 (1,10)	0.572
Wind speed	Pre egg laying/inshore	1998-2009	0.001 (1,10)	0.969
Wind direction	Pre egg laying/inshore	1998-2009	0.78 (1,10)	0.399
Sea surface temperature	Pre egg laying/offshore	1998-2009	0.13 (1,10)	0.723
Chlorophyll a	Pre egg laying/offshore	1998-2009	0.28 (1,10)	0.609
Sea surface height	**Pre egg laying/offshore**	**2000-2008**	**16.34 (1,8)**	**0.004**
Sea surface height anomaly	**Pre egg laying/offshore**	**2000-2009**	**13.85 (1,8)**	**0.006**
Zonal wind	Pre egg laying/offshore	1998-2009	0.85 (1,10)	0.379
Meridional wind	Pre egg laying/offshore	1998-2009	2.70 (1, 10)	0.131
Wind speed	Pre egg laying/offshore	1998-2009	1.14 (1,10)	0.311
Wind direction	Pre egg laying/offshore	1998-2009	2.85 (1, 10)	0 122
Sea surface temperature	Wintering	1998-2008	10.57 (1, 9)	0.331
Chlorophyll a	Wintering	1998-2008	0.41 (1, 9)	0.538
Sea surface height	**Wintering**	**1999-2008**	**6.83 (1, 8)**	**0.031**
Sea surface height anomaly	**Wintering**	**1999-2008**	**7.90 (1, 8)**	**0.023**
Zonal wind	Wintering	1998-2008	0.24 (1, 9)	0.638
Meridional wind	Wintering	1998-2008	0.35 (1, 9)	0.569

Wind speed	Wintering	1998-2008	4 81 (1, 9)	0.056
Wind direction	Wintering	1998-2008	0.002 (1, 9)	0.959
Sea ice extent	mean yearly/ offshore	1979-2007	2.30 (1,27)	0.141

The relationship between ocean data, egg-laying and survival of chicks

Once we identified the trends in environmental variables that corresponded to the trend in egg laying, we incorporated these into a model set according to the temporal scale likely to be most relevant to breeding effort i.e. wintering and pre egg laying. This approach was used to determine which environmental trend, if any, was most closely correlated with the decline in breeding effort. We used generalised linear models (GLM) in R (version 2.10.0, R Development Core Team 2009) with Gaussian distribution and considered identity, log and inverse link functions to fit a series of linear models to the data. Models were weighted according to Akaike's corrected information coefficient (ΔAICc) following Burnham and Anderson (2001). ΔAICc values of < 2 imply that the models have substantial support. Values of 2 < ΔAICc < 7 imply some support and ΔAICc > 7 imply support for that model. The AIC is a useful measure as it is valid for the comparison of non-tested models which allows models with different link and distributional assumptions to be compared (Bradshaw, et al. 2004). Significance of best-fit model terms was tested using analysis of deviance.

Finally, to test if any of the environmental variables were influential during the chick rearing period, the number of chicks fledged per year (n = 6) was compared to the temporally specific range of environmental variables and analysed using a GLM.

Results

Rate of egg laying and survival of chicks

Rate of egg laying displayed a significant exponential rate of change of –15% per year. ($y = -15.3 \pm 0.01x + 317.5 \pm 22.5$, $F_{1,5} = 186.3$, $p < 0.01$, $R^2 = 0.969$) (Fig. 6.2a), (Chapter 2). No linear trend was detected when comparing mean chick survival between years ($F_{1,4} = 0.08183$, $p = 0.789$, $R^2 = 0.00$) although there were years of both good and poor reproductive performance (Laplace approximation, Gaussian distribution, $Z_{1,6} = 2.76$, $p = 0.05$) (Fig 6.2b).

Trends in ocean data

Of the 25 individual variables assessed for linear trends, four displayed comparable trends to the rate of egg laying for the relevant spatial regions (Table 6.1). These were wintering SSH ($F_{1,8} = 6.83$, $p = 0.03$) and SSHa ($F_{1,8} = 7.9$, $p = 0.023$), and pre-egg laying SSH ($F_{1,8} = 16.34$, $p = 0.004$) and SSHa ($F_{1,8} = 13.85$, $p = 0.006$). All demonstrated increasing trends for the measured time series (Fig. 6.3). Correlation analysis demonstrated that SSH and SSHa for both pre-egg laying and wintering were highly correlated (0.99 and 0.99) as SSHa is a function of the SSH. Subsequently, as the best measure of variability, SSHa was selected as the parameter for analysis in the model set.

The relationship between ocean data, egg-laying and survival of chicks

The model set for the GLM included the variables density (density of birds with eggs per square metre), pre-egg laying SSHa, and wintering SSHa with additive and interaction combinations of these model terms. Identity link was used as an examination of the residuals revealed this to be the most appropriate. Model selection identified the best fit model which related the number of eggs laid in a

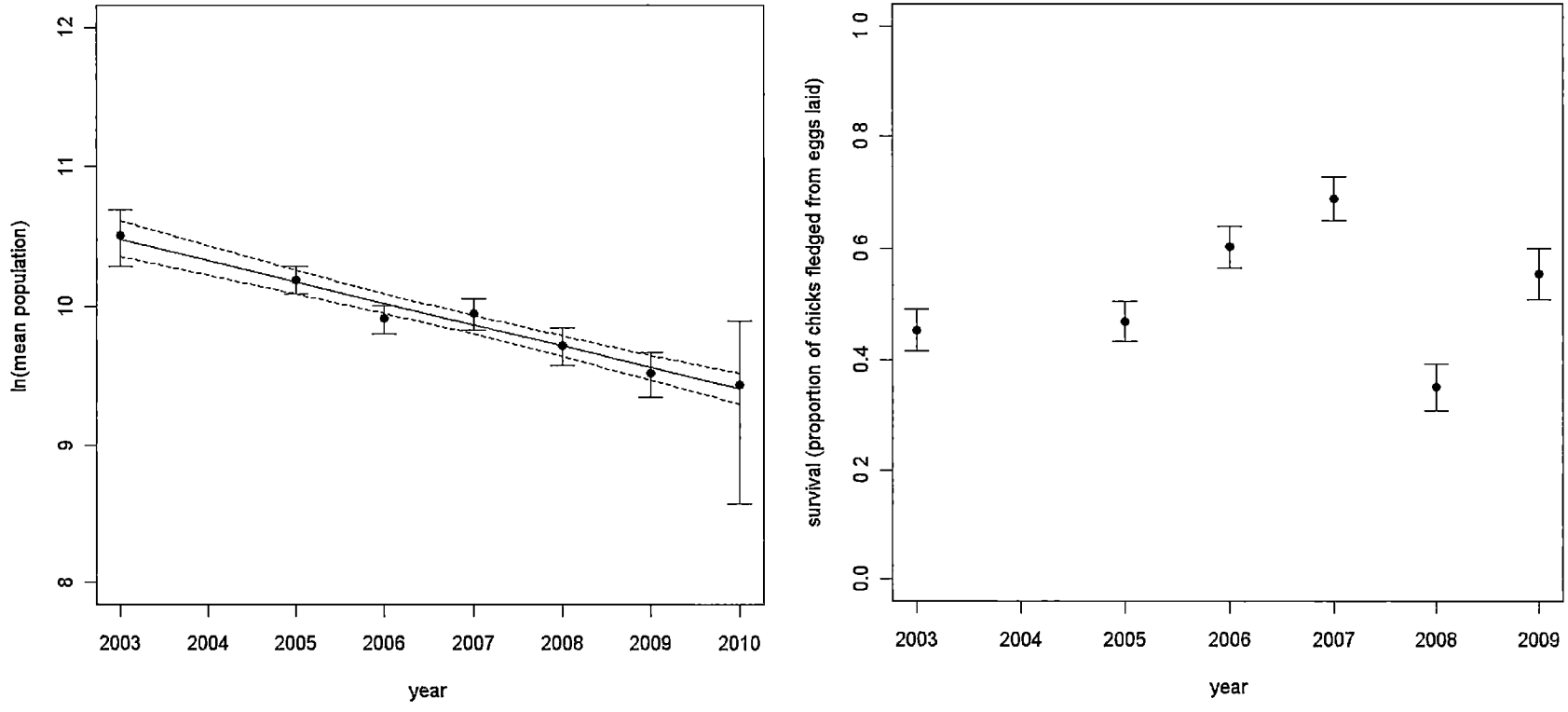


Fig. 6. 2. a) Rate of egg laying of Wedge Island shearwaters from 2003–10 showing an exponential rate of change of –15.2% per annum. Vertical bars represent standard errors and lines around the trend represent the 95% confidence interval; and b) proportion of chicks fledged from eggs laid between 2003 and 2009.

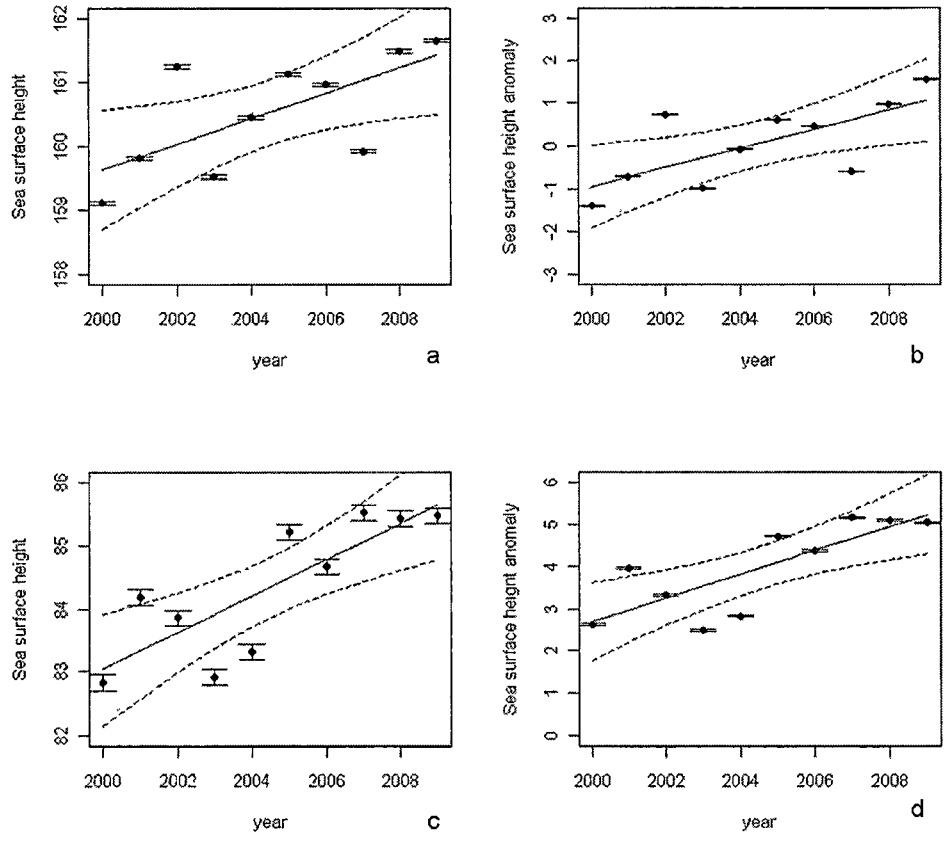


Fig. 6. 3. a) SSH trend during Winter in the Bering Sea; b) SSHa trend during Winter in the Bering Sea; c) SSH trend during the pre-egg laying period in the Southern Ocean offshore foraging boundary; and d) SSHa trend during the pre-egg laying period in the Southern Ocean offshore foraging boundary. For all plots, error bars represent the standard errors and trend lines show the 95% confidence interval.

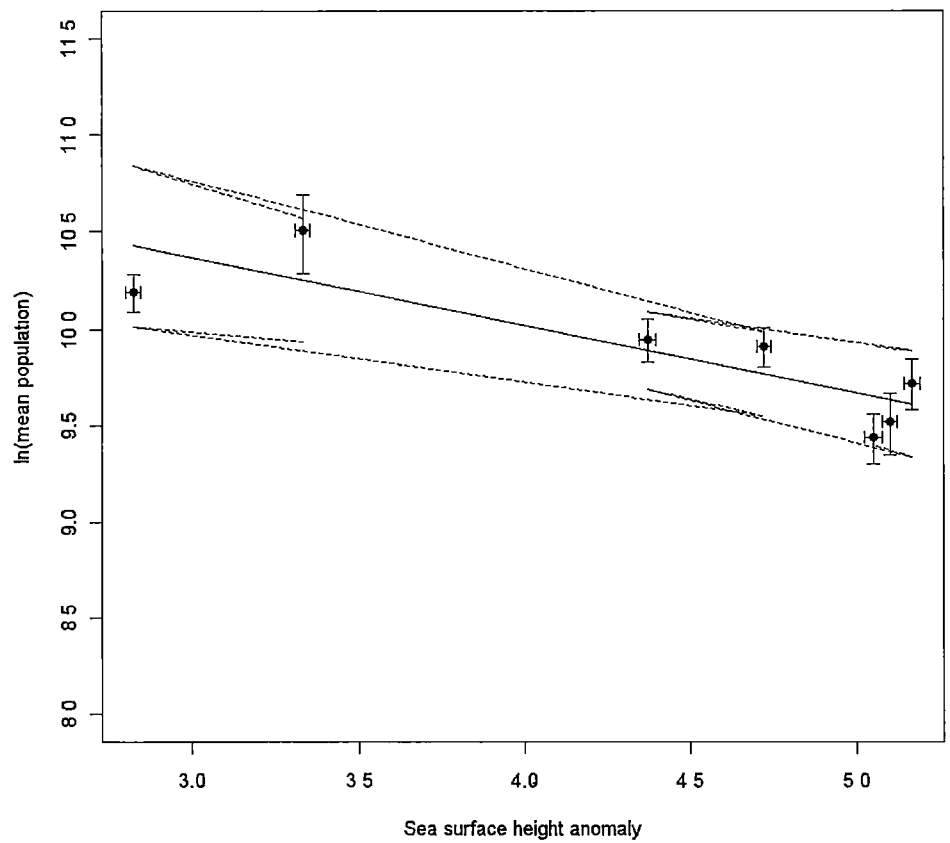


Fig. 6. 4. Sea-surface height anomaly during pre-egg laying in the Southern Ocean and ln(mean population) of short-tailed shearwaters from 2003–10. Error bars represent standard errors, and dashed lines around the trend represent the 95% confidence interval.

year to offshore pre-egg laying SSHa (Table 6.2) and analysis of deviance indicated support for this effect (Dev = 0.13, $F_{1,5}$ = 9.35, p = 0.03) (Fig. 6.4). No support was indicated for the inclusion of the wintering SSHa according to analysis of deviance (Dev = 0.001, $F_{1,5}$ = 0.22, p = 0.66)). Model selection thus indicated that the spatio-temporal scale most relevant to the rate of egg laying was that of the Southern Ocean foraging grounds during pre-egg laying.

As chick survival displayed no trend, all the oceanographic parameters for the chick rearing period for both the inshore and offshore spatial regions were combined into the model set. Also included in this set was a null model (survival~1) which assumes no relationship between chick survival and the tested parameters. The null model was the best fit for the observed values (Table 6.3) and thus we were unable to determine any link between oceanographic variables during the chick rearing period and any relationship they may have to chick survival.

Table 6. 2. GLM results for pre-egg laying and oceanographic variables with k = number of model parameters, Log likelihood, Akaike's corrected information criteria (AICc), delta (AICc) and percent deviance of the model.

model	k	LogL	AICc	dAICc	pcdev
density~sshaOff	**3**	**14.30**	**-14.61**	**0.00**	**65.15**
density~sshaWint	**3**	**10.77**	**-7.53**	**7.07**	**4.28**
density~sshaWint+sshaOff	**4**	**14.67**	**-1.34**	**13.27**	**68.61**
density~sshaWint*sshaOff	**5**	**24.35**	**21.30**	**35.90**	**98.03**

Table 6. 3. GLM results for chick survival and oceanographic variables with k = number of model parameters, Log likelihood, Akaike's corrected information criteria (AICc), delta (AICc) and percent deviance of the model.

Model	k	LogL	AICc	dAICc	wAIC	pcdev
success~1	2	4.75	-1.5	0	0.7937	0
success~Offshore chick rearing wind_sp	3	6 09	5.83	7 33	0.0203	35.9197
success~Offshore chick rearing wind_z	3	5.69	6.63	8.13	0.0136	26.794
success~Offshore chick rearing wind_m	3	5.45	7.1	8.6	0 0108	20.846
success~early chick rearing SOI	3	5.31	7 38	8.88	0 0094	16.9929
success~Inshore chick rearing wind_sp	3	5.24	7.53	9.03	0 0087	14.9426
success~Inshore chick rearing wind_z	3	5.23	7.54	9 04	0 0087	14.8356
success~Offshore pre egg laying SST	3	5 21	7.59	9 09	0.0084	14.0796
success~Offshore pre egg laying wind_z	3	5 12	7.76	9.26	0.0077	11 6218
success~Offshore pre egg laying wind_sp	3	5.09	7.82	9.32	0.0075	10.6814

Discussion

Understanding the nature of the relationship between environmental variability and population can be difficult as changes may affect different demographic parameters (Weimerskirch et al. 2003). An increase in adult mortality or a decrease in adults choosing to breed will have a direct effect on breeding population estimates whereas effects on breeding success, which reduce chick survival, will have a lagged effect on population size (Wooller et al. 1992). The rapidity at which the decline in egg laying has been observed, and simultaneous lack of trend in breeding success (rather than decline), suggest either an increase in adult mortality or a reduction in the number of birds choosing to breed.

While published data is scarce on population trends of seabirds in south-east Australia, there is evidence that the decline may not be occurring in isolation. A small colony located within 100 km of Wedge Island has shown a reduced burrow occupancy from more than 50% in 2002 to 16% by 2010. Longer time series data from 1997–2010 from four islands in the Furneaux group at the centre of the short-tailed shearwater breeding distribution demonstrate no long-term change in annual burrow occupancy ($F_{1,10} = 0.84$, $p = 0.38$, $R^2 = 0.08$, K. Carlyon, unpublished data). However, data from the same time scale as the Wedge Island study are demonstrating an analogous trend ($y = -3.5 \pm 0.77 + 7204x \pm 1576$, $F_{1,4} = 21.3$, $p = 0.01$, $R^2 = 0.80$). Furthermore, additional unpublished data has described a decline of Gibson's albatross (*Diomedea gibsoni*) in two colonies in New Zealand, occurring between 2005 and 2008 at rates of –6.1% p/a and –12.2% p/a with environmental variation in the Tasman Sea hypothesised as a likely contributor but not yet explored (Elliot & Walker unpublished data). Therefore, an increasing body of evidence is accumulating to suggest that we may be observing a synchronised, large-scale change in seabird breeding effort that may be related to environmental factors.

Long-lived animals such as seabirds often live in environments dominated by stochastic variation. Subsequently, for long-lived species, high environmental variability favours the selection of flexible breeding effort that will observe years of high and low reproductive output (Erikstad et al. 1998). Experience is related to

breeding effort in short-tailed shearwaters (Bradley et al. 2000), and we have observed that their foraging behaviour is flexible during the chick rearing with shifts in diet and foraging location that were not directly linked to reproductive success (Chapter 5). For the six year time series analysed here, we detected no trend in chick survival although the small-time series has low power to detect trends and should therefore be interpreted with caution.

Trends in ocean data

Large changes in SSH in the Australian-Antarctic Basin (which extends from the Kergeulen Plateau at about 60° E, to below New Zealand at about 160° E) have been reported between 1992 and 2007, with the change associated with a southward shift of the Polar Front (PF) and the southern Antarctic circumpolar current front (SACCF) of up to 60 km (Sokolov & Rintoul 2009b). These changes are not unique to this area with increases in SSH also being reported in the Atlantic and Australian sector of the Southern Ocean (Morrow et al. 2008). In the Pacific, both increases and declines have been observed (Sokolov & Rintoul 2009b). Also influencing the more northerly parts of the offshore foraging bound and the inshore areas exploited by shearwaters, is the South Pacific sub-tropical gyre. This reached a peak of SSH in 2003 (decreasing in 2004–05) related to the decadal intensification of wind-stress curl east of New Zealand, in turn associated with the decadal increase in the atmosphere's Southern Annular Mode (Roemmich et al. 2007).

Changes in SSH can be brought about by changes in water mass properties or changes in circulation (e.g. movement of fronts) (Sokolov & Rintoul 2009b). Deep changes in the Antarctic Zone temperature-salinity structure are likely to be contributing to the observed sea level rise (Morrow et al. 2008). The deep ocean warming observed has been associated with sea level rise at least 21° south of Tasmania and while it has been associated with the southward frontal movements and redistribution of water masses, it is unknown whether the water mass characteristics themselves have altered (Morrow et al. 2008). However it is fairly certain that the southward movement of ACC fronts (60 km on average) is not

associated with warming and freshening of atmospheric fluxes, but with changes in ocean circulation (Sokolov & Rintoul 2009b).

The relationship between ocean data and egg-laying

Increase in SSH may be related to a number of mechanisms as it is a measure of heat content of the water column, currents and eddies (Hyrenbach et al. 2006) and as such describes many processes that could be biologically relevant to predators. Decadal variability in the sub-tropical gyre has been hypothesised to link to a decline of 87% in the New Zealand hoki fishery (Bradford-Grieve et al. 2004). Enhanced Ekman convergence (a depression of the ocean's thermocline), combined with a downward displacement of isopycnals (surfaces of constant potential water density) described by Roemmich et al. (2007) provide a possible physical mechanism that would be consistent with a reduction in the surface-layer nutrient supply. This would subsequently affect primary production. However, a decrease in primary productivity due to the enhanced Ekman convergance and displacement of isopycnals is unlikely to be the sole mechanism by which predators may be influenced by the SSH increase. We detected no corresponding trend with Chlorophyll a (as our proxy for primary productivity) and the SSH increase suggesting that the two are not explicitly linked.

The observed southward shift of fronts is another mechanism that could affect predator survival or foraging success. This shift could hypothetically increase foraging effort, as an increase in distance to a foraging zone effectively reduces food availability due to the increase in travelling time (Durant et al, 2007). A 60 km southward movement of fronts appears minimal for a species that can travel hundreds of kilometres in a day. However, based on the mean travel speed of 8.6 km h^{-1} during the pre-egg laying stage, an increase in travel of 60 km could theoretically reduce foraging time by up to 15 hours per long foraging trip. Changes in SSH may alter absolute energy availability differently in different seasons. Consequently, if the increase in travel time was also related to a change in distribution and abundance of prey, or in the ability of the predator to detect prey owing to upper level mixing, then a seemingly small change could result in large scale effects such as those that we are observing.

We detected no linear relationship with wind direction or speed corresponding with the increase in SSH reported. Isolating the mechanism most biologically relevant to decline in the rate of egg laying is difficult without more specific information about the fine scale foraging locations of these birds across the time scale at which the decline has been recorded. The complex nature of marine ecosystems makes it unlikely that the same mechanism has been responsible in each successive season. Rather, it is likely to be a synergistic effect of multiple mechanisms in which the final result has been decreased food availability for predators in general and short-tailed shearwaters for this colony specifically.

Short-tailed shearwaters have not previously been reported as displaying non-investment in breeding due to predictive, pre-breeding signals of habitat quality (Bradley et al. 2000) and in any given year, breeding effort is related to age and experience. Our identification of the pre-egg laying temporal scale and the Southern Ocean spatial scale relates most strongly to the decline of breeding birds. This may infer that our observations are related to increased adult mortality related to an inability to sustain body condition after undertaking the migration back to the feeding grounds, as opposed to a reduction in the numbers of birds investing in breeding.

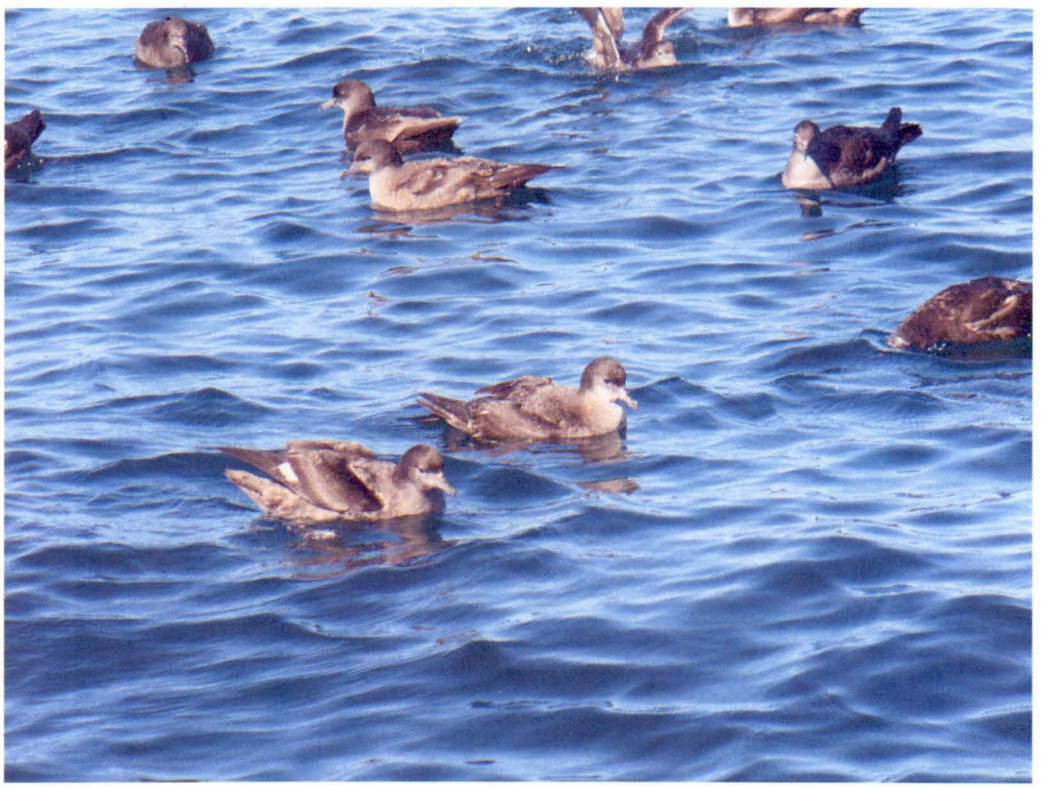
Seabird distribution is linked to a range of meso-scale (100–1000 km) features and hydrographic fronts (Hunt Jr & Schneider 1987; Nel et al. 2001; Hyrenbach et al. 2006; Wolf et al. 2009). Large-scales (> 1000 km) can therefore encompass a range of meso-scale features (Weimerskirch 2007) that may be permanent or transient (Hyrenbach et al. 2006). Here, we demonstrate that when the specific foraging boundaries of a species are known, effects can be detected at large scales. A longer term trend for increasing SSHa during the pre breeding, large scale foraging locations of Wedge Island short-tailed shearwaters was correlated with a decline in breeding bird numbers, a decline which may be reflected in other short-tailed shearwater populations throughout their distribution. While marine predators have shown to be variable in their responses to short-term environmental variation such as SST and SOI (Barbraud & Weimerskirch 2003; Nevoux et al. 2010), population declines can result in areas that exhibit long lasting

changes in environmental conditions (Barbraud & Weimerskirch 2001, 2003). We have demonstrated that correlations with population trends are observable at large spatial scales and that long-term environmental variation may be affecting the breeding rates of one of the most abundant seabird species in the Southern Ocean.

Acknowledgments

Permission to do this research was provided by the University of Tasmania Ethics Committee (A0008138) and under permit (FA 05151) from the Nature Conservation Branch of Tasmanian Parks and Wildlife Service. We thank the many dedicated volunteers for assistance in the field. Some or all of the data used within this paper were obtained from the Australian Antarctic Data Centre (IDN Node AMD/AU), a part of the Australian Antarctic Division (Commonwealth of Australia). These data are described in the metadata record "The maximum extent of sea ice in the southern hemisphere by day and by winter season" Raymond, B. (2009).

Chapter 7



Chapter 7

Synthesis and Conclusions

The broad aim of this study was to describe the population demography of short-tailed shearwaters in relation to intrinsic (*i.e.* density dependent) and extrinsic factors (*i.e.* resource availability). This study determined that the number of short-tailed shearwaters breeding on Wedge Island has been steadily declining, representing an exponential rate of change of –15% between 2003 and 2010 (Chapter 2) and that this decline has not been affected by onshore habitat characteristics (Chapter 2) or by the effect of researchers working in the colony (Chapter 3). I demonstrated that short-tailed shearwaters utilise a vast area of the Southern Ocean during the breeding season, that the characteristics of foraging behaviour are related to the stage of breeding (Chapter 4) and that foraging is flexible in relation to prey availability (Chapter 5). Finally, I detected a correlation between the decline of breeding birds and a large-scale increase in Sea-Surface Height anomaly in the Southern Ocean. The following chapter places this research within the context of research in other species, explores the possible contributors to the decline in terms of density dependent effects and environmental influences, and discusses the limitations of the study before making recommendations for future research in this species.

Population trends of Southern Ocean seabirds

A cornerstone of life-history theory is the prediction that parents should balance their reproductive effort against their own chance of future survival. In highly variable environments, selection may then favour the evolution of life-history traits that display high adult survival and low fecundity (Stearns 1977). Continuation of this theory suggests that for a long-lived species, less investment will occur in unfavourable conditions as a reduction in adult survival effectively reduces the ability to invest in the future when conditions may improve (Hirshfield & Tinkle 1975). Trade-offs represent fitness costs arising when a beneficial change in one trait is linked to a detrimental change in another (Stearns 1989). As trade-offs generally occur only when food is limited, it has been predicted that high environmental variability that may influence the distribution and abundance of resources available to long lived species, may favour the selection of flexible breeding effort (Erikstad et al. 1998).

These life history traits are observed in many pelagic seabirds which tend to be long-lived (15–70 years) and integrate environmental variability over large spatial and temporal scales (Smith et al. 1999). Therefore, measuring seabird population demography (*i.e.* population trends, breeding effort, reproductive output and prey consumption) can provide information about resource distribution and abundance in both large spatial and temporal scales. Describing population trends is a simple way of linking environmental factors to their direct effects. While high adult survival and flexible breeding effort can effectively buffer populations against small-scale changes in food availability (which can be detected as lagged effects in population trends), reductions in adult survival, particularly in breeding females can rapidly reduce the overall population size (Russell 1999; Eberhardt 2002; Oro et al. 2003).

The monitoring of population trends provides information critical to identifying conservation problems at an early stage as well as suggestions for possible solutions (Thomas 1996). However, unravelling the mechanisms driving population trends is typically difficult. Population trend data often cover relatively short time periods, and unless the trends occur rapidly and are reliably measured,

objectively determining the directionality of the trend can be problematic (Thomas 1996; McMahon et al. 2009). Confounding factors are often present such as the effect of the investigator (Durant et al. 2009) and sampling error (Holmes & Fagan 2002) and there are often multiple drivers of population trends *i.e.* intrinsic effects (density regulated) and extrinsic effects (such as environmental variation and its effects on food availability). Given these difficulties, continued monitoring of population demography in tandem with contextual data such as spatio-temporal use of habitat, behavioural observations and use of resources provide a way to measure the effects of environmental variation (natural or human induced) and anthropogenic factors such as habitat encroachment on trophic interactions.

The observed downward trend of in the numbers of breeding short-tailed shearwaters on Wedge Island fits within the context of population trends in other Southern Ocean seabirds, with a number of species displaying significant changes in their distribution and phenology (Parmesan & Yohe 2003). Population trends in marine predators however, are not manifesting uniformly (Inchausti et al. 2003) with some species increasing (*e.g.* king penguin (*Aptenodytes patagonicus*), (Croxall, Trathan, & Murphy 2002), and some declining (*e.g.* sooty albatross (*Phoebetria fusca*), Delord et al. 2008), while others remain stable (Appendix 1). Some species, such as the black-browed albatross (*Thalassarche melanophris*) and the Southern giant petrel (*Macronectes giganteus*), are reporting contrasting trends across their distribution (Micol & Jouventin 2001; Terauds et al. 2005; Poncet et al. 2006; Quintana et al. 2006).

While published data on the trends of short-tailed shearwaters from southern Australia are scarce, evidence would suggest that similar declines are occurring in a colony at Fort Direction in south-east Tasmania, which is within 20 km of the Wedge Island breeding site. Burrow occupancy at Fort Direction has declined from over 50% to 16% between 2002 and 2010 (Carlyon, unpublished data). In contrast to this study and the Fort Direction census, longer time series data from 1997–2010 from four islands in the centre of the short-tailed shearwater breeding distribution demonstrate no long-term change in annual burrow occupancy ($F_{1,10} = 0.84$, $p = 0.38$, $R^2 = 0.08$, Carlyon, unpublished data). However, data from the same time scale as the Wedge Island study are demonstrating an analogous trend

($y = -3.5 \pm 0.77 + 7204x \pm 1576$, $F_{1,4} = 21.3$, $p = 0.01$, $R^2 = 0.80$). While I detected similar trends at equivalent temporal scales, these should be treated cautiously as short-tailed shearwaters may breed for up to 27 years after entering the breeding population (Bradley et al. 1989), and therefore fluctuations in breeding effort are likely over the duration of their lifespan. Hence, there is a necessity for long-term data sets to accurately assess the true directionality of population trends (de Little et al. 2007). Relating the two data sets is also difficult due to the difference in methods use to assess population status (*i.e.* rate of egg laying for the Wedge Island study vs burrow occupancy for the Furneaux group).

Given that the time scale assessed in this study may not be sufficient to identify if this is a natural cycle in breeding effort or not, tantalising evidence remains that the trend observed in the Wedge Island short-tailed shearwaters may be widespread. In support of my interpretation, more unpublished data has described a decline of Gibson's albatross (*Diomedea antiopodensis gibsoni*) in two colonies in New Zealand, occurring between 2005 and 2008 at rates of –6.1% and –12.2% per year with environmental variation in the Tasman Sea hypothesised as the likely cause but not yet explored (Elliot & Walker). Therefore, an increasing body of evidence exists that the population demography of seabirds are changing across a range of distributions. In all cases, the causes for observed increasing or decreasing trends are rarely clear but are tending to occur in one of two categories: 1) direct anthropogenic effects such as by-catch from fisheries and habitat encroachment and 2) indirect effects such as environmental variation. However, before exploring these effects, density dependent processes need to be considered.

The effect of intrinsic processes in describing population trends

Disentangling intrinsic from extrinsic processes can be difficult as density dependent effects may mask or accentuate the detection of population trends (Crick 2004). Furthermore, populations will tend to regulate themselves after short or long-term changes in particular aspects of a species' demography. For example, a long-term study of short-tailed shearwaters on Fisher Island demonstrated a decline of breeding birds between 1955 and1970, a 15 year trend that was cautiously, but not conclusively, attributed to the effect of investigators. A

subsequent partial recovery of numbers occurred after 1970 (Bradley et al. 1989). Similarly, emperor penguins displayed transient trends in survival rates that led to a population decline in Terre Adelie, Antarctica. The decline stabilised at a lower population level once survival rates recovered (Barbraud & Weimerskirch 2001). In general, unravelling the combined factors and mechanisms is usually only possible through long time series data encompassing a range of population densities (deLittle et al. 2007). Generation time in short-tailed shearwaters is long, and adult mortality increases with age (Bradley et al. 1991). Subsequently, natural cycles in reproductive success are expected over long temporal scales and the seven year time series that I analysed for the Wedge Island shearwaters is not sufficiently long to conclusively disentangle intrinsic and extrinsic effects.

Given that the time series is short, there is little current evidence to suggest that density dependent effects are contributing to the observed decline in breeding birds at Wedge Island. Short-tailed shearwaters often occur in high densities around Tasmania of up to 1.04 burrows m^2 (Naarding 1980) and the density of birds on Wedge Island is comparatively very low (0.2 burrows m^2). Furthermore, when burrow occupancy was at its peak in 2003, only 62% ± 3% of available burrows in the surveyed area were occupied which would indicate that, although most burrowing seabird colonies are never at 100% occupancy (Bradley et al. 2000; Scott et al. 2008), the island is capable of sustaining larger densities of birds and has done so in the past. I observed no significant changes in the vegetation cover over the duration of the study and no decrease in the amount of preferred habitat type. Given the static nature of the breeding substrate during the period of data collection, the low burrow density and low occupancy, the evidence collected in this study would suggest that intrinsic factors are not the mechanism behind the observed trend.

Direct anthropogenic effects on population demography

When refining hypotheses to explain observed changes in the population demography of species, it is important where possible, to remove confounding factors that may influence the interpretation of trends (Caughley & Gunn 1996). One of these confounding factors is the effect of investigators, which is one of the

most easily measurable and most ethically significant factors. However, the testing of investigator effects is still lacking in some studies (Wilson & McMahon 2006). The nature and magnitude of investigator effects vary within and between species and should therefore be assessed on a case by case basis (Casper 2009). The influence of investigators on the growth of short-tailed shearwater chicks was previously quantified at various levels of handling (Saffer et al. 2000) and found to have no effect. The long-term Fisher Island study cautiously attributed a decline to the presence of investigators (Bradley et al. 1989), but this was never fully explored. Therefore, prior to this study, minimal information was available on the possible effect of investigators on key-life history traits such as nest site fidelity in short-tailed shearwaters.

In a transect survey such as the one employed in my study, a decrease in nest site fidelity due to researcher disturbance might result in birds being displaced to burrows outside of the measured quadrats. This could reduce the number of birds detected within quadrats and bias consequent population estimates. Previous work on Leach's storm petrel (*Oceanodroma leucorhoa*), a burrowing Procellariiformes that displays similar nest site fidelity to short-tailed shearwaters demonstrated that weekly or daily disturbance reduced nest site fidelity by 37% in contrast to birds disturbed only once during breeding. Adults displaced from their nests due to disturbance in one season, were found breeding the following season at an average of 26 m from their original nest site (Blackmer et al. 2004). Therefore, in the context of explaining the observed decline in breeding birds on Wedge Island, it was important to rule out any effect of investigators on nest site fidelity. Data from multiple years were necessary to be confident in any conclusions that I drew as the presence of investigators may be exacerbated in years when environmental conditions are poor (McMahon et al. 2008). As this study spanned both 'good' and 'poor' breeding years and found no effect of the investigator, it has allowed the removal of the investigator as a confounding effect in the attempt to pinpoint an agent of the reduction in breeding numbers. Importantly, it has also contributed a baseline at which meaningful data can be obtained with minimal disturbance to the animals concerned.

Fisheries by-catch is both an agent of decline and another potentially confounding factor in the attempt to measure variation in population demography. Currently, fisheries by-catch is probably the largest contributor to the declines of Procellariiformes in the Southern Ocean (Butchart et al. 2004). Numerous species such as the wandering albatross (*Diomedea exulans*), southern fulmar (*Fulmarus glacialoides*), white-chinned petrel (*Procellaria aequinoctialis*) and flesh-footed shearwater (*Puffinus carneipes*) have declined due to by-catch in fisheries (Weimerskirch & Jouventin 1998; Micol & Jouventin 2001; Priddel et al. 2006; Barbraud et al. 2008) and by-catch can also exacerbate existing population declines (Scott et al. 2008). The complexity of pelagic ecosystems ensures that population trends are rarely driven by single mechanisms and this is why multi-disciplinary studies are required to identify linkages (Micol & Jouventin 2001).

Short-tailed shearwaters have been documented as by-catch in 14 net fisheries, 5 longline fisheries and 1 trawl fishery and it has been suggested that between 4.2–21.1 million birds have been killed during these interactions in the last 50 years (Uhlmann et al. 2005). Migratory species such as short-tailed shearwaters may also be subject to increased pressure from association with fisheries as their trans-hemispheric distribution means they overlap with peak fishing periods in both hemispheres. Most of the by-catch of shearwaters were reported in the driftnet fisheries, most of which have ceased since 1991 and it could be inferred that by-catch pressure for shearwaters has reduced in the last 20 years. Longline, gillnet and trawl fisheries continue to report shearwaters as incidental by-catch although the numbers are presumed to be insignificant given that these methods involve less interaction of birds with fishing gear, and their operations occur outside of the birds' occurrence intervals (Uhlmann 2003). However, risks for shearwaters still exist and there are major gaps in knowledge about which fisheries pose the most threat. Quantitative estimates of the influence of fisheries on observed population trends weren't possible and fisheries interactions remain a confounding factor or possible agent of decline in this study. However, considering the change in fisheries operations during the last 20 years, by-catch is unlikely to be the cause of the observed trend.

Linkages between environmental variability and population demography

During Chapter 2, I discussed a number of possible hypotheses to identify some of the mechanisms behind the observed trends in the decline of shearwaters on Wedge Island. Of these hypotheses, the influence of environmental variation is the most likely. However, the intermediate steps by which environmental variation could be contributing require further clarification. This can be found by directly linking the physical environment to population demography by means of spatio-temporal foraging behaviour.

Studies of foraging location can reveal information on large to meso-scale resource distribution in locations that would otherwise be difficult to assess using traditional means, such as direct surveys of prey distribution (Ancel et al. 1992). However, functional relationships between marine predators, particularly seabirds, and their biotic and abiotic environments have remained difficult to quantify due to the wide geographic ranges they inhabit and the difficultly in measuring prey distributions at sea (Tremblay et al. 2009). Telemetry studies provide the essential link between population demography and the environment by providing spatially explicit knowledge on at-sea distribution and movements of marine predators. Foraging locations of many smaller seabird species have been largely unrecorded due to the size of telemetry devices, and yet the smaller species such as sooty and short-tailed shearwaters whose populations are estimated as several tens of millions (Warham & Wilson 1982; Skira et al. 1996) have the potential to consume significant marine resources in both the Southern and northern oceans (Shaffer et al. 2006).

In long-lived species with delayed onset of reproduction and high levels of parental investment, parents should invest less in years with unfavourable breeding conditions so as to maximise the likelihood of survival to future breeding opportunities (Stearns 1992; Erikstad et al. 1998). When facing nutritional stress early in the breeding season, birds will either abandon the breeding attempt or reduce their clutch size (Drent & Daan 1980). As petrel species only lay one egg (Lack 1968), then non-breeding by experienced individuals represents the maximum clutch reduction to maintain body condition. This has been observed in such species as blue petrels, wandering albatross and common eiders (Coulson

1984; Weimerskirch 1992; Chastel, Weimerskirch, & Jouventin 1995). However Bradley, Wooller, & Skira (2000), determined that short-tailed shearwaters are more likely to 'bet-hedge' *i.e.* invest in breeding in less favourable conditions, than abandon the breeding attempt prior to egg laying. Their research would therefore indicate that the reduction in the numbers of breeding shearwaters on Wedge Island is more likely to be caused by increased adult mortality than non-breeding.

The most prominent life-history trade-off involves the cost of reproduction. It has two major components, costs paid in survival and costs paid in future reproduction (Stearns 1989). As there are temporal scales at which this trade-off can occur, obtaining information on the spatial scales at which seabirds operate during this temporal frame, provide a means of linking seabirds to their environment. While little information on the at-sea movements of short-tailed shearwaters was available, previous tracking work on both short-tailed shearwaters and the closely related sooty shearwater occurred only during the chick-rearing phase (Klomp & Schultz 2000; Shaffer et al. 2009). By tracking birds from September through to March, I demonstrated that movements at sea changed throughout the course of the breeding season with use of the Southern Ocean, foraging patterns, and behavioural modes displaying marked differences between pre- and post- egg laying (when the birds were constrained to the breeding sites).

At sea movements of upper trophic predators such as seabirds change as they associate with fronts where they find favourable feeding conditions (Bost et al. 2009). This may be due to one of two processes. Firstly, enhancement of local primary production increases prey at the fronts and secondly (Hunt et al. 1990), convergence processes may aggregate prey at the fronts (Spear et al. 2001). During the pre-egg laying stage, long trips by short-tailed shearwaters were characterised by slower travel speeds, higher latitudes and a high rate of area restricted search behaviour (ARS). Foraging at this time-period occurred generally away from the major fronts and within Australian shelf and coastal waters of temperatures between 8 °C to 20 °C. Less foraging occurred within the sub-Antarctic zone (SAZ) and polar frontal zone (PFZ). The foraging behaviour at this time was consistent with exploitation of a number of prey types. The level of ARS infers that prey was patchily distributed within the Australian shelf and coastal

waters, or that birds were not using previous experience to exploit known productive regions. Rather, they employed behavioural modes in order to maximise foraging efficiency. This was in direct contrast to foraging behaviour once egg laying had occurred.

During incubation and chick rearing, long foraging trips typically displayed a more looping pattern. This pattern has been identified in other seabirds (Sagar & Weimerskirch 1996; Hull et al. 1997; Weimerskirch et al. 2005, 2007). Shelf and coastal waters were exploited less during post-investment long trips with the majority of foraging focused within the SAZ and PFZ, to the extent of the Antarctic sea-ice. The temporal change in foraging behaviour is consistent with other species. Grey-headed albatross (*Thalassarche chrysostoma*) focused their foraging in the SAZ and PFZ during chick rearing after previously exploiting more northerly waters during the pre-egg laying stage and incubation Nel et al (2001). Southerly foraging may provide choices of warm and cold eddies at a range of distances from the breeding site that closer inshore may be degraded or depleted by less mobile predators. The selected foraging region therefore represents a compromise between energetic requirements of chicks and body condition of the parents.

Long-lived species such as seabirds may develop an additional energetic advantage by remaining faithful to regions of high productivity (Bradshaw et al. 2004), with the constraint of returning to the breeding site to provision chicks, experienced breeders will draw on prior knowledge of regions of high productivity. Prior to egg laying, when adults are re-establishing body condition to invest in reproduction, foraging strategies can be more flexible with adults having more time, able to be at sea for longer and able to be more selective in their foraging regions. After reproductive investment has occurred, birds are limited by the need to return to the central breeding site and may subsequently draw on prior knowledge in order to maximise foraging efficiency.

Diet represents the intermediary step between extrinsic factors and population demography in marine predators, *i.e.* environmental variation *per se* does not directly affect the life-history of marine predators, rather it is the effect of

environmental variability on the distribution and quality of resources. Therefore, changes in population size reflect temporally distinct, multi-scale factors (Jenouvrier et al. 2003). Traditional methods for studying diet, such as stomach sampling, have been problematic for pelagic seabirds as they typically represent a 'snapshot' of individual diet, often restricted to when parents have returned to land to feed their chicks (Inger & Bearhop 2008). Furthermore, for seabirds that employ bimodal feeding strategies, stomach samples do not represent adult diet at all, but rather prey items passed to chicks (Forero & Hobson 2003; Cherel et al. 2005a). Depending on the tissues analysed, the analyses of stable isotopes provide information not only at longer temporal ranges but isotopes also convey information on the relative importance of prey assimilation as compared to ingestion (Inger & Bearhop 2008).

Geo-location (GLS) has provided insight into the spatial use of the ocean by smaller predators, that could not previously be tracked using the heavier satellite devices. Despite the coarse spatial resolution (200 km per day, when compared to 1–3 km for satellite telemetry (Shaffer et al. 2005)), resolution is improving with the inclusion of SST in estimations of location and the introduction of Bayesian statistics (Sumner et al. 2009). GLS has been particularly informative about the long-range movements of birds outside the breeding season (Shaffer et al. 2006; González-Solis et al. 2007), and also provided information on temporal changes in spatial foraging during the breeding season (Shaffer et al. 2009). However, cost is still a limitation of GLS and can in turn limit the availability of meaningful sample sizes (Ropert-Coudert et al. 2004; Burger & Shaffer 2008).

The use of biochemical markers, such as naturally occurring stable isotopes, is an indirect method of tracking spatial foraging of animals. Carbon 13 ($\delta^{13}C$) reflects the Carbon levels at the base of the food chain (DeNiro & Epstein 1978; Kelly 2000; Cherel & Hobson 2007). Therefore, it can be used to estimate food source location as phytoplankton inshore, typically have higher levels of Carbon than those offshore (Kelly 2000). Stable isotopes have been used to establish spatial foraging locations in a number of species (Best & Schell 1996; Cherel, Hobson, & Weimerskirch 2000; Cherel & Hobson 2007). While providing no indication of longitude, their estimate of latitude has shown to be accurate with good prior

knowledge of the species biology (Cherel & Hobson 2007). Indirect methods such as stable isotope analysis are advantageous as sampling of tissues is minimally invasive and cost effective. Therefore meaningful sample sizes are not a limiting factor.

The two techniques, geo-location and stable isotope analysis, used in tandem, support and reinforce each other by combining the accuracy of geo-location with the high sample size of stable isotopes. Subsequently I can be confident about the large-scale foraging ranges detected in this study. As with the GLS information, diet during incubation and chick rearing was representative of birds exploiting resources in a range of water masses from Australian shelf and coastal waters to the SAZ and PFZ at the ice-edge extent. The isotopic signatures of short-tailed shearwaters monitored over four years demonstrated plasticity in foraging range and prey consumption, that was not reflected in chick survival or fledging mass. Flexibility in foraging behaviour and prey consumption has been previously been demonstrated for short-tailed shearwaters during the winter foraging period (Hunt et. al 2002) and in other top predators such as pinnipeds (Weise et al. 2006).

When comparing the information obtained during the diet study to the observed decline, interpretation is inhibited due to sampling relating only to the post-egg laying phase of breeding. Considering the significant differences documented during between pre- and post-egg laying of tracked birds, any future stable isotope analysis of short-tailed shearwaters from Wedge Island should sample during early incubation, in order to obtain prey information on the pre-egg laying phase. In addition, chick blood samples should be taken in order to obtain information on resources closer to the breeding colony. Chick samples are representative of short trips by adults during chick provisioning and thereby provide information on the assimilation of resources close to the breeding colony (Weimerskirch & Cherel 1998), information currently lacking in this study.

Whilst diet may provide the intermediate link between environmental variation and population demography, caution needs to be applied in terms of using direct diet as a measure of environmental variability. This is because the physiological response of a predator to a change in prey distribution and/or abundance is rarely

linear (Durant et al. 2009). Animals in most circumstances are unlikely to reflect subtle or continuous changes due to buffering behavioural attributes such as the ability to increase effort in times where foraging or flying may be more difficult (Cairns 1987). They may however, provide greater information at threshold levels *i.e.* reductions in resources availability that signal changes in the environment from 'good' to 'bad' or *vice versa* (Montevecchi 1993; Piatt et al. 2007). This, with the continued use of diet, in concert with other measures such as reproductive effort, reproductive success and telemetry studies, will all aid in providing a clearer understanding of the interactions between seabirds and their environments.

Ultimately, upper trophic consumers are dependent on the function of physical oceanographic processes affecting light levels, surface temperatures and the magnitude of nutrient recycling from deep layers. These are the mechanisms that drive bottom-up processes within pelagic ecosystems (Richardson & Schoeman 2004). Changes in physical oceanography appear to be related to changes in atmospheric circulation (Mann & Lazier 2006) which result in cyclical climate events (such as El Nino Southern Oscillation (ENSO) events, or the Pacific Decadal Oscillation (PDO)). Both these phenomena have shown to affect population demography and behaviour in upper trophic consumers (Barbraud & Weimerskirch 2003; McMahon & Burton 2005). Physical oceanography is linked to primary productivity (phytoplankton) via a number of mechanisms that are still not fully understood. However, central to the linkage is the impact of weather on the intensity of ocean mixing (and the reverse, ocean stratification) (Hays et al. 2005).

In combination with natural climate cycles, the last 150 years has observed increased anthropogenic influence superimposed on natural climate fluctuations through global climate change (Hindell et al. 2003). Anthropogenic climate change has the potential to influence bottom-up processes by altering distribution and abundance of base level organisms. Pico-plankton (*e.g.* coccolithophores), which dominate autotrophic biomass in warmer waters, have shown to be extremely sensitive to changes in temperature (Wright et al. 2009). The coccolithophore *Emiliana huxleyi,* was absent, or almost absent in waters below 60° S in 1983–84 and 1994–95. Surveys conducted in 2002–06 have determined it is now present

at levels of 100 cells mL^{-1} at latitudes of 60–65° S. (Cubillos et al. 2007). A change in the size spectrum of Southern Ocean phytoplankton would be expected to have serious consequences for krill and other herbivores that are adapted to a diet of the smaller nano- and micro-plankton (Wright et al. 2009).

Biological changes such as alterations in the distribution of phytoplankton assemblages, are occurring in response to large-scale changes in the physical oceanographic marine environment. Perturbations include changes in sea-ice extent and increases in SSH in both the northern and Southern Oceans in the last 20 years (Atkinson et al. 2004; Roemmich et al. 2007; Sokolov & Rintoul 2009a). During this study, I identified a corresponding trend between an increase in SSH in the Southern Ocean during the pre-egg laying stage of breeding, with the decline in breeding bird numbers on Wedge Island. Prior to egg laying, foraging strategies are more flexible and foraging more selective as adults are able to be at sea for up to 70 days before returning to the breeding colony (Nel et al. 2001). Therefore, at this time, individual foraging strategies should be able to compensate for variation in prey distribution and abundance more effectively than once egg laying has occurred and birds are constrained by the necessity of returning to the breeding site for incubation shifts or chick feeding. While foraging strategies are flexible once breeding has occurred (Chapter 5), it is therefore difficult to determine the biological mechanisms between physical oceanographic processes and the decline of breeding birds during the most theoretically flexible stage of breeding. Enhanced Ekman convergence and a downward displacement of isopycnals which serves to decrease primary productivity has been suggested as one possible explanation by which increased SSH may effect biological systems (Roemmich et al. 2007). However, I detected no corresponding trend with primary productivity for the analysed time series.

Remote measuring of primary productivity is not necessarily the best predictor for the distribution and abundance of preferred prey for upper trophic consumers. As demonstrated by the increase in *E. huxleyi* in polar waters during the last 15 years, productivity may still be high, but the ecosystem dynamics may alter due to changes in phytoplankton assemblages. For example in a study of Adelie penguins by (Beaulieu et al. 2009), an early fast sea ice retreat in Adelie Land,

Antarctica during 2006–07 increased primary productivity by 30%. This in turn, was expected to result in increased krill production. However, owing to the mismatch between the phytoplankton bloom and krill recruitment in that year (with a prevalence of non-preferred pico-phytoplankton dominating primary productivity), krill recruitment was low and the penguins switched to a diet of mostly fish. This did not result in any significant changes in reproductive success and in line with other studies, demonstrates that marine predators display variability in their responses to short-term environmental variation (Barbraud & Weimerskirch 2003; Nevoux et al. 2010).

The intermediate responses of lower trophic consumers to environmental variability are difficult to predict and may have contrasting effects on upper trophic consumers. Short-tailed shearwaters demonstrated plasticity in their foraging behaviour and their foraging locations during incubation and early chick rearing. However, without corresponding diet information on the pre-egg laying period it is difficult to speculate on the specific mechanisms by which an increase in SSH across the pre-egg laying foraging locations may be affecting the rate of egg laying. While the increase in SSHa during the wintering period of shearwaters in the Bering sea was not correlated with the decline in breeding birds, there may still be implications from that physical process that are influencing the pre-egg laying stage.

Possible mechanisms, in addition to the decrease in primary productivity, could include:

1. A mixing of the upper layers changing prey distribution;
2. Upper level mixing increasing of the surface layers of the ocean increasing the difficulty for visual predators to see and catch prey; or
3. A southward movement of fronts increasing foraging effort as I determined that a 60 km shift in fronts could theoretically reduce foraging time by 15 hours per long foraging trip.

More likely, it is a combination of the above effects. The migration period of the short-tailed shearwater is energetically expensive as birds have to cross the

relatively unproductive central Pacific Ocean (Nicholls et al. 1998). Their survival to breed, on their return to the breeding colonies is then dependent on the resources available to them at that time. If resources are insufficient at this time, birds may starve before breeding can commence. In the case of the Wedge Island short tailed shearwaters, it would be naïve to assume that the trend is driven by one mechanism only. It is the complex nature of marine ecosystems that makes it unlikely that the same mechanisms are responsible in each successive season but rather we are observing a synergistic effect of multiple mechanisms which is increasing adult mortality.

Final conclusions

Ecological changes in the phenology and distribution of plants and animals mediated by changes in the environment are occurring across the globe and have been documented for a wide range of species (Parmesan 2006). In the Southern Ocean, changing population trends in relation to various environmental factors, both direct and indirect, are occurring in numerous species (Appendix 1). Therefore, it is not surprising to have documented changes in shearwater numbers as they are one of the most abundant predators in the Southern Ocean. The number of breeding short-tailed shearwaters on Wedge Island declined throughout the duration of the study, a decline that was also observed throughout the distribution of this species during this same time period. Oscillations in population size in response to natural climate cycles have been documented in Procellariiformes (Lyver et al. 1999; Thompson & Ollason 2001; Dunlop et al. 2002; McKechnie et al. 2009). However, none of these studies demonstrated a reduction in numbers as rapid as I documented here. While some Procellariiformes do not attempt breeding in unfavourable conditions (Coulson 1984; Weimerskirch 1992; Chastel et al. 1995), this has not been demonstrated in short-tailed shearwaters (Bradley et al. 2000). Therefore, indications are that the observed decline is related to increased adult mortality.

While the short-tailed shearwaters in this study demonstrated plasticity in both their prey consumption and spatio-temporal use of foraging grounds, the protracted increase in SSHa as my indication of environmental variability may imply that

consecutive seasons of strong environmental variation are contributing to the observed decline. However, correlation between environmental variables and reproductive parameters does not necessarily imply a cause and effect relationship (Votier et al. 2008; Durant et al. 2009). While I detected a correlation between the number of birds breeding on Wedge Island and an increase in SSHa in the Southern Ocean during the pre-egg laying stage, it does not definitively follow that this is related to the observed trend.

As environmental changes may affect different demographic parameters (Weimerskirch et al. 2003) and the response variables may be direct (*i.e.* an increase in adult mortality or a decrease in adults choosing to breed) or lagged (*i.e.* reductions in breeding success) (Wooller et al. 1992), it is likely that multiple processes are contributing to the decline of shearwaters on Wedge Island. It is probable that all the hypotheses outlined in Chapter 2, *i.e.* source-sink population dynamics, emigration due to a decline in habitat quality, incidental by-catch and offshore environmental variation are contributing in some way. This colony should continue to be monitored, in addition to others within the species distribution. Long-term data sets will eventually determine if this is part of an oscillation in breeding numbers or a response to more long-lasting shifts in environmental conditions. Chick diets should be obtained in addition to adult diet corresponding to the pre-egg laying period. Marking of birds within the colony will assist in making stronger conclusions as to the effect of emigration. Further telemetry studies will aid in detecting inter-annual differences in foraging behaviours.

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Appendix 1. Table of population trends of seabird species. Ranges span the southern and northern hemispheres and describe species, location, time-span, trend, status, possible reasons and study source. Abbreviation EV in trend column is environmental variation

Species	location	time span	trend %	status	reasons	source
Adelie penguin (*Pygoscelis adeliae*)	Terre Adelie, Antarctica	1985-1999	>3 5 p/a	increasing	EV	(Micol & Jouventin 2001)
Emperor penguin (*Aptenodytes forsteri*)	Terre Adelie, Antarctica	1985-1999	-0.9 p/a	stable	n/a	(Micol & Jouventin 2001)
	Terre Adelie, Antarctica	1963-2008	-1.2 p/a	decreasing	variation in sea ice extent	(Barbraud & Weimerskirch 2001)
King penguin (*Aptenodytes patagonicus*)	Ile de la Possession (Iles Crozet) colony 1	1960-1996	+15 p/a	increasing	variation in sea ice extent	(Barbraud & Weimerskirch 2001)
	colony 2	1960-1996	+6.9 p/a	increasing	variation in sea ice extent	(Barbraud & Weimerskirch 2001)
	colony 3	1960-1996	+4.8 p/a	increasing	variation in sea ice extent	(Barbraud & Weimerskirch 2001)
Galapagos penguin (*Spheniscus mendiculus*)	Galapagos Islands	1970-1995	50% in 25 years	decreasing	El nino, la nina	(Boersma 1998)
African penguin (*Spheniscus demersus*)	Namibia	1996-2001	-3.25 p/a	decreasing	El nino, la nina	(Kemper et al. 2007)
Rockhopper penguin (*Eudyptes chrysocome*)	Campbell Island, Southern Ocean	1942-1985	94% total	decreasing	EV	(Cunningham & Moors 1994)
Wandering Albatross (*Diomedea exulans*)	Bird Island, South Atlantic	1961-1989	-1.0 p/a	decreasing	fisheries by-catch	(Croxall et al 1992)
	Iles Crozet, South Indian Ocean	1966-1986	between 2.6-8 1 p/a	decreasing	fisheries by-catch	(Weimerskirch & Jouventin 1998)
	Macquarie Island, Southern Ocean	1966-1993	8.1 p/a	decreasing	fisheries by-catch	(Mare & Kerry 1994)
Grey headed albatross (*Thalassarche chrysostoma*)	Bird Island, South Atlantic	1975-1991	1.8 p/a	decreasing	fisheries by-catch	(Prince et al. 1998)
Amsterdam Albatross (*Diomedea amsterdamensis*)	Amsterdam Island, Southern Ocean	1984-2004	+6.7 p/a	increasing	recovery from by-catch	(Pannekoek & Pannekoek 2006)
Gibson's Albatross (*Diomedea antiopodensis*)	Antipodes Islands, New Zealand	1996-2004	+5.1 p/a	increasing	n/a	(Elliot & Walker)
	Antipodes Islands, New Zealand	2005-2008	-6 1 p/a	decreasing	changes in Tasman Sea	(Elliot & Walker)
	Auckland Islands, New Zealand	1996-2004	+2.2 p/a	increasing	n/a	(Elliot & Walker)
	Auckland Islands, New Zealand	2005-2008	-12 2 p/a	decreasing	changes in Tasman Sea	(Elliot & Walker)
Atlantic yellow nosed albatross (*Thalassarche chlororhynchos*)	Gough Island, South Atlantic	1986-2003	-2.1 p/a	decreasing	fisheries by-catch	(Cuthbert et al. 2003)
Black browed albatross (*Thalassarche melanophris*)	Macquarie Island, Southern Ocean	1977-2003	n/a	stable	n/a	(Terauds et al. 2005)
	South Georgia Island, Southern Ocean	1990-2004	-4.0 p/a	decreasing	fisheries by-catch	(Poncet et al. 2006)

	remaining distribution	n/a	unknown	unknown	n/a	
Buller's albatross (*Thalassarche bulleri*)	Snares Islands, New Zealand	1992-2004	+3 2 p/a	increasing	n/a	(Sagar & Stahl 2005)
Indian yellow nosed albatross (*Thalassarche carteri*)	Amsterdam Island, Southern Ocean	1978-2006	-1.9-4.9 p/a	decreasing	avian cholera	(ACAP 2009)
Short-tailed albatross (*Phoebastria albatrus*)	Torishima Island, Japan	1954-2008	+6.8 p/a	increasing	n/a	(U S. Fish and Wildlife Service 2008)
Sooty albatross (*Phoebetria fusca*)	Iles Crozet, South Indian Ocean	1980-2006	-4.2 p/a	decreasing	fisheries by-catch	(Delord et al. 2008)
	Marion Island, Southern Ocean	1987-2005	-2.5-4.9 p/a	decreasing	fisheries by-catch	(Delord et al. 2008)
Sooty shearwaters (*Puffinus griseus*)	New Zealand	1969-2001	-1.72 p/a	decreasing	fisheries by-catch, EV	(Scott et al. 2008)
Short-tailed shearwater (*Puffinus tenuirostris*)	Wedge Island, Australia	2003-2010	-15 p/a	decreasing	undetermined	this study
	Furneaux islands, Australia	1947-2010	n/a	stable	n/a	(Carlyon)
Flesh footed shearwater (*Puffinus carneipes*)	Lord Howe Island, Australia	1978-2002	19% total	decreasing	fisheries by-catch, habitat loss	(Priddel et al. 2006)
	Marion Island, Southern Ocean	1985-2008	variable	both	n/a	(ACAP 2009)
Cory's shearwater (*Calonectris diomedea*)	Selvagem Grande, north-east Atlantic	1975-2005	+4 6 p/a	increasing	recovery from poaching	(Granadeiro et al. 2006)
Cape petrel (*Daption capense*)	Terre Adelie, Antarctica	1985-1999	+2 3 p/a	stable	n/a	(Micol & Jouventin 2001)
Snow petrel (*Pagodroma nivea*)	Terre Adelie, Antarctica	1985-1999	+0 9 p/a	stable	n/a	(Micol & Jouventin 2001)
Southern Giant Petrel (*Macronectes giganteus*)	Terre Adelie, Antarctica	1985-1999	-3.9 p/a	decreasing	direct human disturbance	(Micol & Jouventin 2001)
	Isla Arce	1987-2004	n/a	stable	n/a	(Quintana et al. 2006)
	Isla Gran Robredo	1990-2004	n/a	increasing	n/a	(Quintana et al 2006)
Northern giant petrel (*Macronectes halli*)	Macquarie Island, Southern Ocean	1997-2008	+4 8-6.9 p/a	increasing	increased food source	(ACAP 2009)
Southern fulmar (*Fulmarus glacialoides*)	Terre Adelie, Antarctica	1985-1999	+0.4 p/a	stable	n/a	(Micol & Jouventin 2001)
	Terre Adelie, Antarctica	2963-2002	+0.35 p/a	stable	some relationship EV	(Jenouvrier et al 2003)
White-chinned petrel (*Procellaria aequinoctialis*)	Iles Crozet, South Indian Ocean	1991, 1998	-1 65 p/a	decreasing	fisheries by-catch	(Barbraud et al. 2008)
	South Georgia Island, Southern Ocean	1983, 2004	-1.76 p/a	decreasing	fisheries by-catch	(Berrow, Croxall, & Grant 2004)
	Prince Edward Islands	1997-2000	-14 1 p/a	decreasing	fisheries by-catch	(Nel et al. 2002)
South polar skua (*Catharacta maccormicki*)	Terre Adelie, Antarctica	1985-1999	>3 5 p/a	increasing	response to increasing penguins	(Micol & Jouventin 2001)